出國報告(出國類別:研究)

中、新生代雙孔類爬行動物化石群 演化、古生態與古環境研究 (II)

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出國期間:	2014/04/14~2014/04/28
報告日期:	2014/05/19

_ 摘要 —

本次係執行教育部核定本館 (103) 年度<<非營業特種基金 — (二) 社教機構作業 基金部份>> 編號第 11 號之計畫。赴大陸地區進行一系列、延續性,經過審慎、精心 設計之野外地層剖面量測、脊椎動物化石及伴生無脊椎化石與古植物化石之標定、採 集;與室內進行關鍵且重要、豐富化石群標本之仔細量測、檢視、修復,特徵之定碼 (coding),以及伴隨該項動物群化石產生之重要論文初稿,經共同作者進行修訂。並且 進行下一年度計畫路線之規劃,以及針對以往(含本次)研究工作進行嚴謹之檢討,作 為爾後工作之指準。

由計畫主持人與共同主持人,二人前往執行。並且會同團隊合作研究人員,分別進 行各階段不同剖面、個別化石群之探究。包括了中科院古脊椎動物與古人類研究所(北 京,IVPP)、貴州地質探勘院(貴州興義)、北京大學地質研究所、雲南楚雄州川街恐 龍研究中心等,多位研究人員與協力技術人員協同野外採集工作。

— 目次 —

摘要		00
目的		01
過程		02
心得與	建議	.05
附錄一	路線圖	.07
附錄二	三疊紀海生爬行動物建構略圖	.08
附錄三	附圖	.09
附錄四	近年研究成果代表	.19

— 本文 —

目的:

2014年4月14日至4月28日,前往大陸黔滇地區,進行移地研究計畫 <<中、新 生代雙孔類爬行動物化石群演化、古生態與古環境研究>>,係執行教育部核定本館 << 非營業特種基金 --(二)社教機構作業基金部份>> 編號第11號之計畫。依計畫規定, 赴雲南、貴州,人數2人,天數15天,預算金額 120千元而進行。

目地明確,係一系列、延續性,經過審慎、精心設計之野外地層剖面量測、脊椎動物化石及伴生無脊椎化石與古植物化石之標定、採集;與室內進行關鍵且重要、豐富化石群標本之仔細量測、檢視、修復,特徵之定碼 (coding),以及伴隨該項動物群化石產生之重要論文初稿,經共同作者進行修訂。並且進行下一年度計畫路線之規劃,以及針對以往(含本次)研究工作進行嚴謹之檢討,作爲爾後工作之指準。

累積多年來計畫所獲致成果堪稱豐碩(如附件,請參見論文初稿)。具體而言,其目的有下列諸項:(一)我們合作團隊想要深入探究中生代的三疊系中、晚期(距今約240-200百萬年前),在古地中海(Paleo-Tethys)的東緣,即位居今日黔西南與滇東南地區的古環境與古生物地理區位(Paleo-environment and Paleo-biological niche);(二)我們要建構起三疊系中、晚期這整個區域之海爬行動物群的系譜關係,並且細化建立牠們精確的支序圖(cladogram),作爲這一領域在國際間進一步研究之指準圖像;(三)我們在系列工作中,終極目的在宏觀的重建全球中生代早期之三疊紀雙孔類爬行動物(Diapsid Reptile),在從陸地再次下水(從海口相、濱海相,到封閉淺海相,乃至開闊海域相)的關鍵演化事件中,其各個支序起源、變異、趨異多樣性、分支,形式爾後之式微與最終滅絕之斷代細節。

本次行程,依據上述目的,循例由計畫主持人與共同主持人,二人前往執行。並且 會同團隊合作研究人員,分別進行各階段不同剖面、個別化石群之探究。包括了中科院 古脊椎動物與古人類研究所(北京,IVPP)、貴州地質探勘院(貴州興義)、北京大學

地質研究所、雲南楚雄州川街恐龍研究中心等,多位研究人員與協力技術人員協同野外 採集工作。本次行程,配合多邊合作之事前協調,於本年4月14日至4月28日,總計 依原訂計畫15日(含去程與返程)完成。剩餘工作,團隊之大陸研究人員持續進行。 經費則依本館核定之出差額度內支用,編列總計約新臺幣壹拾貳萬元。依國內差旅標準 支付後,尙餘經費核實交回。

過程

檢附雲貴地區,研究部份區域與路程作為指引,詳述如次:

行程:依照擬訂之行程(如下表),除些微視野外工作情況調配外,均按路線與地區前往。分成兩大區塊進行。

日期	行程
第一日	臺灣-(過境香港)-昆明。去程。
	租車司機接往祿豐恐龍研究中心。
第二日	工作團隊集結於祿豐。
	行程確認,租車裝備、圖幅等準備事宜。
第三日	往澄江撫仙湖地區。檢視新發掘重要剖面。
第四日至第八日	野外工作於滇東南地區中、晚三疊系地層與化石群。
	(經曲靖,富源地區;師宗、雨汪、羅平地區)
第九日至第十三日	野外工作於黔西南地區中、晚三疊系地層與化石群。
	(越省界,烏沙剖面、興義地區;頂效、興仁地區,
	往北至盤縣地區)
第十四日	野外工作結束,返回祿豐恐龍研究中心,總結野外工
	作項目,擬定下年度行程。
第十五日	昆明-(過境香港)-臺灣。返程
以上	二行程,視實際情況微調更動。

(A) 雲南(滇東南區塊)部份。第一日至第八日。

臺灣過境香港接往昆明。預先訂好租車含司機接機後,經高速路往西到楚雄州 祿豐川街世界恐龍谷,恐龍研究中心。受董枝明教授暨中心主任接待,並與團 隊成員會合。第二日商談本次行程細節,並進行野外工作器材裝備之完善裝車 工作。一切就緒後於 4/16 (三),先往昆明東南方澄江(撫仙湖)地區,檢視 新近發掘寒武紀早、中期重要化石剖面,並進一步了解,近年來針對前寒武瓮 安生物群與寒武紀大爆發澄江生物群研究之進展。由於本館 (NMNS) 最早介 入澄江生物群之特展介紹,以及學術刊物(學報專刊)與第一本圖鑑之發表, 本計畫主持人為主編職位。該項目研究人員熱誠接待、相互探究,並提出嶄新 成果交流展示與科普工作之可能性。

第四日至第八日行程 (4/17-4/21) 經昆曲高速 (G320) 往雲南東南部進行野外 新剖面之檢視、量測、取樣以及重要化石發掘(於當地農民及博物館/陳列館) 之檢視工作。先經曲靖往東達富源地區,隔兩省界限與貴州盤縣遙望,分別屬 於富源生物群與盤縣生物群(爲該地區三疊系最早期、最古老的生物地層。) 富源爲近幾年最重大的發現與發掘。最初由四川成都地調研究人員進行區域填 圖 (mapping) 時發現。開始有計畫之發掘工作。新的小山頭剖面,已經受到 保護與管制。

後轉往師宗(高速路 G78 線),越羅平與雨汪,黃泥河地區,進行經典傳統 剖面之複查工作。羅平地區之化石群位居富源之上層,較為年輕,化石類型與 多樣性遠遠高於前者。仔細之古生態系譜以及古環境工作,多個研究團隊正在 深入進行中。因這時期為乾季,進入小路之剖面較為容易。溪水較淺,地層出 良好,工作基本順利。於第八日結束滇東地區之工作。移往貴州興義市,利用 半日總結資料,並繪作細部地形/地質圖幅,屬內部資料,存檔於中科院研究 室中保存。

(B) 貴州 (黔西南區塊) 部份。第九日至第十三日。

野外工作第九日至第十三日 (4/22-4/26),轉往黔西南。自興義市,與北京大學 地質研究所蔣大勇教授及其研究生會合,隊伍一行,抵達近年挖掘剖面烏沙剖 面檢視,並核對其生物地層細節。興義動物群 (Xingyi Fauna)的烏沙剖面(泥 麥谷村)併同關嶺動物群 (Guanling Fauna)的關嶺國家地質公園剖面;盤縣動 物群 (Panxian Fauna)的新民烏蒙溝國家地質公園剖面;與羅平動物群 (Luoping Fauna)的羅平剖面;綜合涵蓋了中三疊至晚三疊(大約 241 ma 至 220 ma 的二千萬年時距沉積相。)其中烏沙剖面為科學家首次為科研工作而 挖掘的相對完整剖面,涵蓋了竹桿坡段的完整地層。

接續檢視剖面現址搭建臨時修復化石工作間與臨時蒐藏庫房。核對與之前發表 模式標本之比對,與新近發掘標本層位之對比 (correlation) 工作。其間受邀於 興義市市長款待詢問籌建現址博物館事宜。

接續轉往西面頂效地區,參訪貴州龍博物館,檢視傳統楊老命名、保存不全之 諸多模式標本,試圖重新比對新近發掘之完整標本,並且協助討論新博物館/ 陳列館之籌建工作。轉往東北部興仁地區,檢視零星出露剖面及當地農民/老 鄉挖掘之幻龍、海龍與魚龍類標本。

由興仁地區向西轉往盤縣地區。在蔣教授陪同下,檢視經典盤縣動物群指準化 石標本,並量測一些自盤縣地區命名之種屬的模式標本,並且與在鄰近富源地 區、較爲淺水/濱海相之物種比對。

野外工作基本結束於盤縣(第十三日,4/26)。沿高速路(G60)向西,再經富 源,往昆明,返回祿豐川街恐龍研究中心。集結室內,總結黔西南所獲取資料, 歸還野外圖幅。修訂已完成論文初稿,作最終審定,投稿於美國古椎動物學報 中。最後,擬訂明年度工作的初步協議,並接受中心主任董教授安排座談與學 術交流工作。第十五日(4/28)自昆明過境香港返臺,結束本年度工作。

心得與建議:

本年度依既定計畫,接受本館報部核定經費,移地前往雲貴地區進行研究採集工作,為期十五天。工作進行順利完成,達成既定目標,完成初步成果,並且擬定了下階 段之預期發展工作。總結心得與建議事項,列舉數點以供參酌:

(一)大陸在經濟發展快速翻倍成長之因素支撐下,科研經費成倍數加碼。科研單位, 尤其是核心成員團隊不虞經費之匱乏,唯在尋找更強固合作團隊,亟思與國際接 軌,並且在部份強項領域中,企圖引領國際,企圖心強盛。新一代科學家泰半有 國際學習經驗,甚或歐美返中,紮根華夏。在材料資源優勢的有利條件下,發展 迅速驚人,或許遠超出我們想像。

科研上層決策單位,訂大戰略,企圖心旺盛,早已非昔日吳下阿蒙,令人眼界大開,憂喜參半。我們跨海西進,基於數十年線索網路,尙能攜手合作,不卑不亢。 唯內心思索,如何接續綿延。引領後生,薪火相傳,是其憂心之處。此為心得之 一。

- (二)市場經濟運作下,百物競長。所有花費,不論住宿、租車、食物等飛漲下,以本 地出差標準報銷,在實務上有逐漸捉襟見肘之困。唯因往昔與科研人員友好關 係,截(人)長補(己)短,尙能順利達成任務。唯,在接續一代年輕研究人員 與對岸新一代學人的合作中,將逐漸走向西方資本主義式明確權利義務之簽訂。
 "讓利"之策,非上策也。在這樣時空背景變遷下,如何調整策略,或者重新思 索大戰略,當是決策上層重要功課。此為心得之二。
- (三)在合作關係長遠建構之下。彼此優、弱勢漸趨明朗:大陸具備原始材料、標本資源之強大豐富優勢。我輩科研人員受西方嚴謹科學訓練,與遊走科學生涯經驗, 具有高思維、大視野與較全面、較深層洞察。大陸較年輕學者鬥志旺盛、企圖心強大、衝勁十足,不畏阻礙。唯,國際語言、溝通與最新科學理論性動向,困於 資訊相對封鎖實情下,求知若渴。但是領會敏銳,舉一反三,潛力無窮。在西方 科學界分工、協同合作的傳統與默契方面,尙因敬老尊賢,獨占山頭、學派較勁、

"文人"相輕的傳統下,其實質團隊緊密契合度不足。在彼長我消的過程曲線趨勢中,我們科研人員如何善用優勢,建構彼此雙贏機制,既取得契機,又能協助 團隊擠身國際學術舞台,是最上層大戰略。孤單戰鬥、星火零星、個人單兵突圍, 非以小博大之策。此為心得之三。

多年來,本館研究人員,接受專案申請補助,移地前往大陸進行科研工作,若能 形成大戰略下的具方向性、分工協同性、團隊合作性,長期佈局性,而非純然拜 會、參訪、學習,事過境遷的。始可建立較爲緊密、牢靠的長遠合作關係。而此 項經大部嚴謹審查,核實之經費,終究是彼此雙贏,建構大合作關係的終極保障, 心存感激之情,當溢於言表也。





中國華南地塊雲貴地區三疊紀海生爬行動物群					
Fauna Formation Age Marine reptiles					
關嶺動 物群 Guanling Fauna	Wayao Mem.	Carnian early Late Triassic (220+ ma)	Thalattosaurians Ichthyosaurians Sauropterygians Turtle		
興義動 物群 Xingyi Fauna	Zhuganpo Mem.	Ladinian late Middle Triassic (227+ ma)	Thalattosaurians Sauropterygians Protorosaurians Archosaurian		
盤縣動 物群 Panxian Fauna	Guanling Fm.	Anisian early Middle Triassic (234+ ma)	Ichthyosaur Sauropterygians Protorosaurians Archosaurians		
羅平動 物群 Louping Fauna	Guanling Fm.	middle Anisian early Middle Triassic (241+ ma)	Ichthyosaur Sauropterygians Protorosaurians Archosaurians		

中國華南地塊雲貴地區三疊紀海生爬行動物群





















附件四:

雲貴地區三疊紀海生爬行動物最新成果定稿論文 (ms.)

Journal of Vertebrate Paleontology: For Review Only



Dawazisaurus brevis, a new eosauropterygian from the Middle Triassic of Yunnan, China

Journal:	Journal of Vertebrate Paleontology
Manuscript ID:	JVP-2014-0023
Manuscript Type:	Article
Date Submitted by the Author:	10-Feb-2014
Complete List of Authors:	Cheng, Yen-nien; National Museum of Natural Science, Geology; National Cheng Kung University, Earth Sciences Wu, Xiao-Chun; Canadian Museum of Nature, Earth Science; Sato, Tamaki; Tokyo Gakugei University, Natural Science Shan, Hsi-yin; National Museum of Natural Science, Geology
Key Words:	Diapsida, Sauropterygia, Triassic, China, Systematics, Anatomy

SCHOLARONE[™] Manuscripts

Dawazisaurus brevis, a new eosauropterygian from the Middle Triassic of Yunnan, China

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R.H.: CHENG ET AL. -- NEW SAUROPTERYGIAN FROM CHINA

ABSTRACT—Dawazisaurus brevis (gen. et sp. nov.) was described on the basis of a nearly complete skeleton (less than 50 cm in total length) from the Upper Member of Guanling Formation (Anisian) of Luoping County, Yunnan Province, Southwestern China. This new species has a very short trunk comprising 16 vertebrae with very small zygapophyses and an ossified distal carpal 5. Its postorbital region is distinctively longer than the preorbital region, its external naris is closer to the orbit than the anterior end of the snout, its elliptic supratemporal fenestra is as long as but much narrower than the orbit, its moderately developed interfenestral septum on the skull roof is posteriorly narrow and not as broad as the interorbital region, the squamosal process of its postorbital is deeply forked posteriorly, and a fang-like tooth is present separately in the premaxilla and maxilla. Our phylogenetic analyses suggest that *Dawazisaurus* is an eosauropterygian and phylogenetically more closely related to the Nothosauroidea than Pistosauroidea and that it may have had a closer relationship to *Keichousaurus* or *Dianopachysaurus* than to the European pachypleurosaurs or other Chinese pachypleurosaurlike forms. The discovery of *Dawazisaurus* supports the views that the pachypleurosaurs and pachypleurosaur-like forms had an Asian origin and that all Mesozoic aquatic reptilian included here can be grouped in a monophyletic clade in which the Ichthyopterygia, Thalattosauria, and Saurosphargidae are successively close to the Sauropterygia.

INTRODUCTION

The recently discovered Luoping fauna is mainly comprised of a mixture of marine animals, including arthropods (crustaceans, millipedes and limulids), fishes, reptiles, bivalves, gastropods, belemnoids, ammonoids, echinoderms, brachiopods, conodonts, and foraminifers (Hu et al. 2011). It is one of the best preserved Triassic marine fossil treasures known in the world and has been considered to be coeval in age with the Panxian fauna, about 90 km northeast, in southwest Guizhou Province of China, which is suggested by the occurrence of the *Nicoraella kockeli* Zone of conodonts (Hao et al. 2006; Zhang et al. 2009; Hu et al. 2011, 2013). As for vertebrate assemblages, especially the reptilian members in Luoping and Panxian faunas, it is comparable to those known in Europe (such as Mont san Giorgio) but much more diverse than those in North America (such as Nevada). Among the reptiles, sauropterygians appear to be the most common components of the Luoping and Panxian faunas (Jiang et al. 2009, Hu et al., 2011) and best represented by pachypleurosaur-like forms (Jiang et al. 2008; Liu et al. 2011; Wu et al. 2011; Shang et al. 2011; Sato et al., 2013).

We provide here a description and the phylogeny of another pachypleurosaur-like eosauropterygian on the basis of a nearly complete skeleton. The specimen of the new eosauropterygian was collected from the Member II of the Guanling Formation near the Dawazi (Daaozi) Village of Luoping County where two pachypleurosaur-like forms *Dianopachysaurus* Liu et al., 2011and *Diandongosaurus* Shang et al., 2011 were unearthed. It is a small form, with a total length of about 43 cm. The short trunk and some of skull features indicate that the new taxon clearly differs from any known eosauropterygian. The specimen of the new form is housed in NMNS, Taiwan, China.

Interrelationships of many Triassic-aged eosauropterygians, especially pachypleurosaurs, nothosaurs, and a number of pachypleurosaur-like forms found in China during last two decades, have been subject to debate (Rieppel and Lin, 1995; Jiang et al., 2008; Holmes et al., 2008; Liu et al., 2011; Shang et al., 2011; Wu et al., 2011; Cheng et al., 2012a; Sato et al., 2013, 2014; Neenan et al., 2013). This has led to controversial as to the monophyly of some groups such as the Pachypleurosauria and Nothosauroidea (Rieppel, 2000; Cheng et al., 2012a). Despite taxonomic uncertainty to the Pachypleurosauria (sensu Rieppel, 2000 and Liu et al., 2011), the European forms of the Pachypleurosauria (Neusticosaurus, Serpianosaurus, Dactylosaurus, and Anarosaurus) have often formed a clade separated from the Nothosauroidea (sensu Rieppel, 2000) and the Chinese pachypleurosaur-like forms in recent studies, and the term 'European pachypleurosaurs' are used to refer to those four genera below in this study as in Cheng et al. (2012a). The new taxon described here not only adds a new member of the Chinese eosauropterygians, but also provides further information to test the existing hypotheses on phylogenetic relationships among the European pachypleurosaurs, Nothosauroidea, and the Chinese pachypleurosaur-like forms.

Institutional abbreviations—IVPP-Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica, Beijing, China; NMNS-National Museum of Natural Science, Taichung, Taiwan, China.

Anatomical Abbreviations—af, articular fossa; an, angular; ar, articular; as, astragalus; ca, calcaneum; car, caudal rib; cav, caudal vertebra; cax, axial centrum; cl, clavicle;

co, coracoid; cr, cervical rib; cv, cervical vertebra; d, dentary; dc, distal carpal; delt, deltopectoral crest; dr, dorsal rib; dt, dentary tooth; dt3+4distal tarsals 3 and 4; dv, dorsal vertebra; ecg, ectepicondylar groove; enf, entepicondylar foramen; f, frontal; fcr, facet for cervical rib; fd, facet for dentary; fe, femur; fi, fibula; gs, gastralia; h, humerus; int, internal trochanter; il, ilium; im, intermediate; is, ischium; itrf, intertrochanteric fossa; j, jugal; lad, last alveolus of dentary; lcav, last caudal vertebra; m, maxilla; mt, maxillary tooth; n, nasal; nat, neural arch of atlas; nax, neural arch of axis; np, neural spine; p, parietal; pap, paroccipital process; papil, post-acetabular process; pf, postfrontal; pl, palatine; pm, premaxilla; pmt, premaxillary tooth; po, postorbital; poz, postzygapophysis; prf, prefrontal; pzax, post-zygapophysis of axis; prz, prezygapophysis; pt, pterygoid; pu, pubis; q, quadrate; ra, radius; rap, retroarticular process; rfe, right femur; sa, surangular; sc, scapula; so, supraoccipital; sq, squamosal; sr, sacral rib; ti, tibia; v, vertebra; ul, ulna; uln, ulnare; zph, zygosphene; zyg, zygantrum; I to V, metacarpals or metatarsals I to V.

SYSTEMATIC PALEONTOLOGY

Sauropterygia Owen, 1860 sensu Rieppel, 2000

Eosauropterygia Rieppel, 1994

Dawazisaurus gen. nov.

Type Species—*Dawazisaurus brevis ge*n. et sp. nov. **Diagnosis**—As for the type and only species.

Distribution—As for the type and only species.

Etymology—*Dawazisaurus* was derived from the Chinese pinyin of Dawazi (Daaozi) Village near which the famous Luoping Biota has been recently discovered.

Dawazisaurus brevis gen et sp. nov.

(Figs. 1-4)

Holotype—NMNS000933-F034397, a nearly complete skeleton exposed in dorsal view.

Locality and Horizon— Near Dawazi (Daaozi) Village, Luoping County, Yunnan Province, China; Member II of the Guanling Formation, lower Middle Triassic (Anisian). Data in the specimen label did not specify a stratigraphic level of the formation, which were inferred from a literature (Zhang et al., 2009).

Etymology—The specific name is derived from the short trunk which consists of only 16 vertebrae, representing the smallest number of the dorsal series of the vertebral column among known non-placodontian sauropterygians.

Diagnosis—A small eosauropterygian, with a total length of less than 50 cm,

distinguishable from others in the combination of the following characters: trunk short, with 16 dorsal vertebrae; zygapophyses of dorsal vertebrae very small, leading to a butterfly-shaped appearance of neural arch in dorsal view; ossification of distal carpal 5; large nasals meeting each other along their medial length; posterior process of postorbital asymmetrically forked deeply; interfenestral septum of skull roof narrow, narrower than interorbital region; external naris closer to orbit than to anterior end of rostrum; elliptic supratemporal fenestra as long as orbit but much narrower than the latter; posterior margin of skull roof deeply concave; occipital

crest elongate retroarticular process with a pronounced ridge on dorsal surface; a fang-like tooth present in premaxillary and maxillary, respectively; 20 cervical, four sacral, and 37 caudal vertebrae; six carpals and three tarsals; and phalangeal formulae 2-3-4-4-? in forelimb and 2-3-4-5-4 in hindlimb.

DESCRIPTION

NMNS000933-F034397 is articulated and nearly complete. It was preserved in dorsal view, but the anterior portion of the neck was twisted lightly to the left side (Fig. 1A). It reaches a total length of about 43 cm. Measurements for the selected elements of the skull and postcranial skeleton are available in Table 1.

Skull

The skull is well preserved except for areas around the external naris and the right supratemporal fenestra (Fig. 1C, D). Little of the palate and braincase are exposed. Most of the mandible is hidden by the skull. The snout (preorbital region) is shorter than the postorbital portion (to the posterolateral end of the squamosal). The external naris is closer to the orbit than to the anterior tip of the rostrum; its nearly rounded outline is comparable to that of *Dianopachysaurus* (Liu et al., 2011:fig. 3). The oval orbit is large, with rimmed margins. The elliptic supratemporal fenestra is approximately as long as the orbit although it is much longer than wide. The interfenestral region of the skull roof is narrower than the interorbital region as in *Dianopachysaurus*. The large, ventrally open infratemporal fenestra mainly faces laterally

and slightly dorsally. The oval parietal (pineal) foramen is positioned somewhat anteriorly, closer to the anterior than the posterior margin of the supratemporal fenestra. The dorsal surface of the skull roof is commonly smooth although certain fine ridges and grooves are scattered in the frontal and parietal. Sutures between the roof elements are more clearly marked on the left side than the right. The occipital edge of the skull roof is deeply concave.

The large, paired premaxillae form the rostral portion anterior to the external naris. There is no maxillary process below the external naris. The nasal process is moderate long and forms, together with the nasal, the internarial septum. The interdigitated premaxillary-nasal suture is posteriorly positioned in the septum.

The nasal is basically triangular in outline and longer than wide. It meets its counterpart along the midline. The interdigitated nasal-frontal suture is located just anterior to the orbit. Anterolaterally, the nasal broadly enters the external naris.

The frontals are partly fused and consist of a narrow anterior portion and a broad posterior portion. Its anterior end is forked, receives the nasal anteriorly, and meets the prefrontal laterally. Its posterior portion forms a posterolateral process which meets the postfrontal laterally and approaches the supratemporal fossa posteriorly as in many pachynothosaur-like forms such as *Qianxisaurus* (Cheng et al ., 2012a). The frontal-parietal suture is deeply interdigitated.

The fused parietal is goblet-shaped in dorsal view, anteriorly broad and posteriorly narrow. The interfenestral region is narrower than the interorbital region and only 1.2 mm wide at the narrowest place just anterior to the posterior margin of the supratemporal fenestra. The broad anterior portion is concave and forms the medial part of the supratemporal fossa.

Anterolaterally, the parietal contacts the postfrontal and postorbital. The occipital plane is concave; it meets the squamosal in a wavy suture, whereas its suture with the supraoccipital is simple and gently curved.

The maxilla appears to be a triradiate bone. Its anterior process forms the ventral border of the external naris. Its posterior process is slender and abuts against the jugal along the ventral border of the orbit. Its broadened ascending/nasal process forms the posteroventral border of the external naris. Maxillary suture with the prefrontal is oblique.

The prefrontal is crescent-shaped in outline and forms the anterior edge of the orbit. It meets the jugal to exclude the maxilla from the orbit as in some European pachypleurosaurs such as *Anarosaurus* and *Dactylosaurus* (Rieppel, 2000). No suture indicates the presence of a lacrimal. The prefrontal meets the frontal dorsally and the jugal ventrally. In dorsal view, the prefrontal is ridged along the orbital margin.

The jugal is a curved and strap-like bone and medially very concave. It joins the formation of the ventral margin of the orbit. It inserts between the maxilla and prefrontal anteriorly and curves dorsally to form the ventral half of the postorbital bar (Fig. 2A).

The postfrontal is a triangular bone, with a sharp anterior portion as in *Qianxisaurus*. It forms the posterodorsal border of the orbit. Posteriorly, it broadly enters the supratemporal fenestra. The postfrontal/postorbital suture is interdigitated.

The postorbital is characterized by a long and forked posterior process, with the posteromedial fork being nearly twice as long as the posterolateral fork. As in many other eosauropterygians such as the European pachypleurosaurs, the dorsomedial process forms the

lateral half of the postorbital arch between the orbit and supratemporal fenestra. The descending process forms the major part of the postorbital bar between the orbit and infratemporal fenestra.

The large squamosal is comprised of a roof portion, a descending process, and an occipital portion. The anterolateral process of the roof portion is forked and forms the posterior half of the supratemporal arch; its suture with the posterior process of the postorbital is deeply interdigitated. The short medial process of the roof portion extends medially along the posterior border of the supratemporal fenestra and meets the parietal and together forms the posterior border of the fenestra. The descending process appears a broad plate although it is incomplete on both sides. There seems to be a quadratojugal/squamosal suture paralleling to the posterior margin of the infratemporal fenestra on the left side but it could not be confirmed on the right side of the skull, leading to an ambiguous presence of the quadratojugal. Ventrally, the process nearly reaches the quadrate condyle as in *Anarosaurus* and *Dactylosaurus*. The occipital portion is obscured due to the dorsoventral compression.

The quadrate is poorly preserved and only the condylar part of the right side is exposed. The lateral portion of the condyle appears slightly larger than the medial portion.

The palatine and pterygoid of the palate are only partially exposed inside the orbits. Their exact shape and relationships with other palatal elements are unknown.

Exposed or partly visible elements of the braincase include the supraoccipital and opisthotic-exoccipital complex (Fig. 1C, D). The supraoccipital was broken into two pieces; it shows a slightly convex surface with a weakly developed median ridge as in other eosauropterygians such as *Qianxisaurus*. No suture is recognized in the exoccipital-opisthotic

complex; the exoccipital is medially bulged and its paroccipital process becomes narrow and displaced distally. Damage surfaces show some pneumatic spaces inside the bone.

Mandible

Only the posterior portion of the mandible is exposed and available for description. The posterior-most end of the dentary is observed on both sides (Figs. 1B, C; 2A). Posterodorsally, the bone overlaps the surangular and tapers to a pointed end. Posterolaterally, its suture with the surangular and angular is interdigitated. The elongate surangular forms the dorsal half of the posterior portion of the mandible. Anteriorly, the bone narrows and its tip is covered by the upper jaw; posteriorly, it forms the lateral wall of the articular fossa and abuts against the articular in the retroarticular process (Fig. 1C, D). The dorsal margin of the bone is thickened and concave. The external surface of the bone is concave, with some longitudinally oriented fine ridges. The angular is shorter and slightly shallower than the surangular in lateral view (Fig. 2B). Anteriorly, the angular narrows and underlies the dentary. The ventral surface and posterior end of the bone are not exposed. As with the surangular, the angular bears some longitudinally oriented fine ridges and grooves on the lateral surface. The articular is broad and forms most of the articular fossa and the retroarticular process. The articular fossa is divided into two parts, matching the division of the quadrate condyle. The retroarticular process is modestly developed. The process slightly turns dorsally and bears a longitudinal ridge on the dorsal surface.

Dentition

There are five premaxillary teeth, of which the fourth is the largest and fang-like, the fifth is the smallest, and the others are similar in size (Fig. 2A, B). There are 20 maxillary teeth, with seven and five teeth missing in the left and right maxillae, respectively. The eighth maxillary tooth is the largest and fang-like. Compared with the premaxillary fang, the maxillary fang is slightly smaller. Other maxillary teeth are much smaller and of similar size. It is difficult to know the extract number of the dentary teeth and any dentary fang(s) due to the occlusion of the upper jaw. All teeth are sub-conical and curve medially and slightly posteriorly, with fine striations on the crown surface.

Axial skeleton

The vertebral column is complete (Fig. 1A), consisting of 77 vertebrae (20 cervicals, 16 dorsals, four sacrals, and 37 caudals). Compared with *Diandongosaurus* (20 cervicals, 18 dorsals, and three sacrals [Sato et al., 2013]) and *Dianopachysaurus* (20 cervicals, 19 dorsals, and four sacrals) from the same fauna, the new form also has 20 cervicals but only 16 dorsal vertebrae (two or three fewer than the aforementioned two taxa, respectively). The 20th vertebra was considered as the last cervical for the new form because its rib is much shorter than that of the first dorsal vertebrae – the 21st vertebra (Fig. 3A). The four sacral vertebrae were identified on the basis of their rib morphology (Fig. 3C). The tip of the neural spine was damaged in most vertebrae except for posterior-most dorsals, two anterior sacrals, and some of the anterior caudals. Zygapophyseal pachyostosis is evident in the cervical series but weakly developed throughout the other series of vertebrae. All preserved ribs, from the sixteenth cervical to the twelfth caudal, clearly have such pachyostosis.

The proatlas is missing. The atlas is represented by a pair of incomplete neural arches in dorsal view and the other parts of the vertebra are not exposed (Fig. 1C, D). The atlantal neural arch bears a pronounced postzygapophysis, and the neural arch bends medially and may have met the counterpart along the dorsal midline in life. The axis is characterized by the longitudinally broad but low neural spine; much of its centrum is not exposed. Suture between the axial neural arch and the centrum is indistinct owing to fusion. The centrum is weakly constricted and bears a rib facet on the anteroventral side of the centrum.

Cervicals 3 to 20 differ little from each other in morphology except for the size; they become longer and broader posteriorly to the 16th, and then they decrease in length towards the dorsals. The low neural spines are distally thickened and broadened longitudinally such that their distal margins contact each other (Fig. 2C, D). Suture between the neural arch and centrum is not always evident in cervicals 3 to 7, which are the only vertebrae that show the lateral surface. Zygapophyseal pachyostosis in the cervical series is evident. The zygantrum-zygosphene articulation is present above and between the zygapophyses, as shown in cervicals 6 to 8 (Fig. 2C, D). The preserved cervical ribs are double-headed and equipped with an anterior process which is distally free. The posterior cervical ribs become longer and they are evidently single-headed in cervicals 19 and 20.

The 16 dorsal vertebrae are characterized by the small size of their zygapophyses. The width between the postzygapophyses is about 60% of that between the left and right transverse processes (Fig. 3A, B). This ration is considerably smaller than those of the other vertebral series. Within the dorsal series, this ratio becomes somewhat larger towards the sacrum. Unlike in the cervical series, the zygapophyseal pachyostosis is not evident but the transverse processes

of the dorsal series are very stout. The neural spines differ little from those of the posterior cervicals; they are low and their broadened distal margins contact each other. All dorsal ribs are evidently pachyostotic at the shoulder region and they bow posteromedially, with a heart-shaped articular facet. The last three dorsal ribs become gradually shorter and the last one is just slightly longer but slenderer than the first sacral rib (Fig. 3C).

The four sacral vertebrae were identified on the basis of the distally thickened ribs (Fig. 3C, D). They are shorter than most of the dorsals. As in the dorsal series, the broadened distal margins of their neural spines touch each other. The sacral ribs are stout bar-like; they are shorter than the dorsals and, unlike the last two dorsal, tapers off distally. The four sacral ribs converge toward the medial surface of the ilium; neither of their ends is firmly sutured to or fused with the ilium or the sacral vertebrae. The second and third sacral ribs are slightly longer than the other two.

Of the 37 caudal vertebrae (Figs. 1A, D; 3D), the first several caudals are similar in length to the last sacral vertebra and the others become shorter and thinner towards the end. The last caudal is very small, about one-fourth of the preceding one in length, and triangular in outline (Fig. 1B). The last caudal is also triangular in *Diandongosaurus* but about the half of the length of the preceding caudal in that taxon. The neural arches of the caudals are partly sutured to the centra as shown by caudals 13 to 15 (Fig. 3A). The neural spines in the complete caudals are not evidently taller than those of the dorsals, and they did not increase in height but become narrow distally in posterior caudals where they are complete. There are 12 caudals evidently with the transverse processes (caudal ribs) which become shorter towards the posterior end. The first dos not tapers off distally, like the sacrals, but much shorter than the former. The transverse

process becomes very small in caudal 13 and almost reduced in caudals 14 and 15. The processes are sutured to the centrum until caudal 9 and fused with the centrum in caudals 10 to 15, suggesting that NMNS000933-F034397 represents a relatively old specimen. As in *Dianopachysaurus* and many nothosaurs such as *Nothosaurus* of Li and Rieppel (2004), the caudal ribs are pachyostotic and broad, wider than the inter-rib spaces. No chevron is exposed.

The gastralia are largely unexposed, some of them are visible through the ribcage and show no distinct features (Fig. 3B).

Pectoral Girdle and Forelimbs

In the pectoral girdle, the clavicles and scapulae are exposed in dorsomedial view, both coracoids are largely obscured by the covering ribs and vertebrae, and the interclavicle is not exposed (Fig. 3A). The clavicle is ventro-medially narrow and dorso-laterally broad. Its anterolateral margin is convex and lacks an anterolateral process seen in *Diandongosaurus*. As a whole, the bone resembles that of *Dianopachysaurus* (Liu et al., 2011:fig. 4). Laterally, the clavicle broadly overlaps the medial side of the scapular and medially, its relationships with its counterpart of the other side and the interclavicle are not exposed.

The scapula consists of a broadened proximal/ventral portion and a rod-like distal/dorsal blade. The proximal portion is extensively covered by the clavicle and no distinct features are exposed. The rod-like dorsal blade becomes thin and tapers to a point end distally (Fig. 3A), which is different from the blunt tip of *Dianopachysaurus* or *Diandongosaurus*.

Both forelimbs are nearly complete in dorsal view (Figs. 1A; 4B, D). The humerus is bowed posteromedially and the anterolateral margin is slightly concave. The distal end is slightly expanded. On the proximodorsal surface, there is a low but clearly marked crest which may have served for the insertion of the M. deltoideus (Storrs, 1991:fig. 25A). On the distodorsal surface, the entepicondylar foramen is relatively high in position, as seen in *Dianopachysaurus* (Liu et al., 2011:fig. 5). An ectepicondylar groove but not a foramen is evidently present (Fig. 4B). The distal surface is convex; the articular facets for the radius and ulna are clearly divided, with the facet for the latter being slightly concave and much broader than that for the former.

The radius is medially concave and laterally convex, with an expanded proximal end, and the shaft is nearly straight (Fig. 4C). The distal end is slightly expanded, and the distal articular facet is nearly flat, whereas the proximal facet for the humerus is slightly concave.

The ulna is approximately as long as the radius but its shaft is thicker than that of the latter (Table 1). The proximal and distal ends of the ulna are similarly expanded towards the radius as in *Dianopachysaurus*. Like the radius, the medial side of the ulna is concave and the lateral side is convex. Both proximal and distal surfaces are convex.

There are six ossified carpals, i.e., the ulnare and intermedium forming the proximal row and distal carpal 2 to 5 of the distal row (Fig. 4A, C). The ulnare is asymmetrically pentagonal in outline and much smaller than the kidney-shaped intermedium. The latter articulates all other carpals except for distal carpal 5 and its proximal surface is concave. The largest of the distal row is distal carpal 4.

Metacarpals II to V are complete in both forelimbs (Fig. 4A, C). Metacarpal III is the longest (6 mm), followed by metacarpals IV (5.5 mm) and II (5 mm) (Table 1). Metacarpal V is shorter (4 mm) but not thinner than the others. Metacarpal I, damaged in both manus, may be

the shortest (estimated to be 2.5 mm) but it is the most robust (Fig. 4C). The phalangeal formula is of 2-3-4-4-?. The ungual element appears the shortest but is the stoutest phalanx for each digit.

Pelvic Girdle and Hindlimbs

None of the pelvic elements are completely exposed (Fig. 3D, E). The better exposed right ilium shows that it is a short and stout bone with a stub-like dorsal blade that has a reduced post-acetabular process; such a process is entirely lost in *Qianxisaurus* and the European pachypleurosaurs such as *Neusticosaurus* (Sander, 1989). The medial surface of the ilium is slightly concave but ridged around margins. The width of the ilium is much smaller than the total width of the distal ends of the four sacral ribs, which suggests a soft/loose connection between the ilium and sacral ribs. The publis may have been a flat bone; it is broadly covered and no distinct features are available for description. Both ischia show their posterolateral margins, which is highly concave as in many eosauropterygians, such as *Diandongosaurus* and *Dianopachysaurus*. As with the publis, the ischium should have been a flat bone.

Both hindlimbs are well-preserved (Figs. 1A, 4C, F). The femur is in lateral view; its nearly straight shaft is cylindrical, with slightly expanded proximal head. Its anterolateral side is convex and its posteromedial side is concave. The internal trochanter is pronounced but the intertrochanteric fossa is shallow although evident (Fig. 4E).

The fibula and tibia are almost same in length but the shaft of the former is slightly thicker (Table 1). The fibula is preserved in lateral and slightly medial (tibial) view; its shaft bows towards the tibia (Fig. 4C). The unexpanded proximal end of the fibula bears a slightly concave surface for the femoral condyle; whereas the modestly expanded distal end is equipped with two facets for the calcaneum and astragalus. The tibia is preserved in medial (fibular) view, its shaft bowing towards the fibula. Both ends of the tibia are not expanded and each has a concave facet for the femoral condyle proximally and for the astragalus distally.

There are tree ossified tarsals: the calcaneum, astragalus, and a distal tarsal (Fig. 4C, F). The astragalus is the largest, with a shoe-shaped outline. The 'mouth' of the 'shoe' articulates with the fibula proximally, the dorsomedial aspect receives the tibia, and the 'bottom' (the distal side) of the 'shoe' meets metatarsals I to III and the distal tarsal. The distal tarsal distally meets metatarsals III and IV and it should be considered as the fusion of distal tarsals 3 and 4. The lateral (anterior) surface of the three tarsals is depressed.

All metatarsals are preserved in both feet (Fig. 4C, F). The shortest and stoutest is metatarsal I which is less than the half of the longest metatarsal in length (Table 1); metatarsal III and IV are similar in length, and metatarsals II and V are comparable in length. The articulated pes has a phalangeal formula of 2-3-4-5-4. The ungual phalanx is the largest for each digit.

COMPARISON

It is evident that *Dawazisaurus* is not a pistosauroid; it lacks a set of key features of the Pistosauroidea (sensu Rieppel, 2000) such as: no nasal, the braincase deeply recessed below the parietal roof, the squamosals contacting each other behind the parietals, the box-like suspension of the squamosal, the parietal foreman anteriorly displaced, the sagittal crest of the skull table, and distinctively thickened distal end of the dorsal transverse process. The maxillary tooth raw ending in front of the posteroventral border of the orbit, the supratemporal fenestra distinctively small, the pachyostotic dorsal ribs and zygapophyses suggest that *Dawazisaurus* is morphologically more similar to some of the Chinese pachypleurosaur-like forms or the European pachypleurosaurs than to nothosaurs. Up to date, there are about ten pachypleurosaurlike eosauropterygians known from the Triassic of southern China, including some early known taxa (Chinchenia, Young 1965, Kwangsisaurus Young, 1959, Sanchiaosaurus Young, 1965, and *Hanosaurus* Young, 1972). Most of those early taxa are very fragmentary, whereas *Keichousaurus* and four recently described species (*Wumengosaurus*, *Dianopachysaurus*, Diandongosaurus, and Qianxisaurus) are well represented. Therefore, we compared the new form primarily with the European pachypleurosaurs and those well represented Chinese forms. To characterize *Dawazisaurus*, we focus on the comparison of the following features.

 The short trunk. Before comparison, we have to clarify the definition of the last cervical or the first dorsal vertebra. There are usually two ways to define the vertebrae among researchers: (a) considering the vertebrate just in front of the pectoral girdle as the last cervical (such as Rieppel, 1989) and (b) recognizing the vertebra that starts to bear elongate ribs as the first dorsal vertebra (such as Carroll and Gaskill, 1985; Wu et al., 2011; Cheng et al., 2012a). In general, method (a) counts two cervicals fewer and two dorsals more when compared with method (b). There are 16 dorsals in the *Dawazisaurus* as counted in method (b) (Fig. 1A), indicating that it had not only a shortest dorsal series of the vertebral column but also a shortest presacral region (36 vertebrae) among known non-pistosauroid eosauropterygians (Carroll and Gaskill, 1985; Sander, 1989; Rieppel, 1989, 2000; Young, 1958; Wu et al., 2011; Shang et al., 2011; Cheng et al., 2012a).

- 2. Small zygapophyses of the dorsal vertebrae. It is indicated by the width across the prezygapophyses or postzygapophyses, which is approximately half the width across the transvers processes (Fig. 3B, D). Such a proportion is much larger than 2/3 in the European pachypleurosaurs or other Chinese pachypleurosaur-like forms such as *Serpianosaurus* and *Wumengosaurus*.
- 3. Supratemporal fenestra. This fenestra is relatively long, nearly as long as the orbit compared with that of other Chinese pachypleurosaur-like forms such as *Diandongosaurus* as well as the European pachypleurosaurs such as *Neusticosaurus*; in the later the fenestra is much shorter than the orbit.
- 4. The interfenestral septum and elongate supratemporal fenestra on the skull roof. The interfenestral septum between the elongate supratemporal fenestrae is narrower than the interorbital region although it does not become a sagittal crest in *Dawazisaurus* (Fig. 1C, D). This septum is distinctively broader than the interorbital region and the supratemporal fenestrae are small and round in the European pachypleurosaurs such as *Serpianosaurus* and *Dactylosaurus* and some Chinese forms such as *Qianxisaurus and Wumengosaurus*.

The interfenestral septum is relatively narrow and the supratemporal fenestra is also elongated oval in *Keichousaurus* and *Dianopachysaurus* but the former is still broader than interorbital region and the latter is distinctly shorter than the orbit in the two forms.

- 5. The postorbital. The postorbital usually has a strong but structurally simple posterior process. This process enters the infratemporal fenestra in some of the European pachypleurosaurs (such as *Neusticosaurus*) and the Chinese pachypleurosaur-like forms (such as *Qianxisaurus*) but is excluded by the jugal-squamosal contact in others of the aforementioned taxa (such as *Diandongosaurus* and *Wumengosaurus*) from the fenestra. In *Dawazisaurus*, the process is pronounced and enters the infratemporal fenestra, but it is uniquely forked distally to receive the anterior process of the squamosal (Fig. 1C, D).
- 6. The occipital crest (posterior margin of skull roof). In most Chinese pachypleurosaurs (such as *Wumengosaurus*, *Qianxisaurus*, and *Dianopachysaurus*) and the European forms (such as *Neusticosaurus*), the posterior margin of the skull roof is nearly straight or only slightly concave in dorsal view. In contrast, it is deeply concave, nearly V-shaped in *Dawazisaurus* (Fig. 1C, D). A similar condition may be seen in *Dactylosaurus/Anarosaurus* (Sues and Carroll, 1985; Klein, 2009).
- 7. Fang-like tooth. The premaxillary and maxillary also bear fang-like teeth in *Keichousaurus* (Holmes, 2008) and *Diandongosaurus* but the maxillary fang is anteriorly positioned in the two forms, differing from that of *Dawazisaurus* where the eighth maxillary tooth is fang-like. The other Chinese forms and the European pachypleurosaurs do not have any fang-like teeth in both the premaxilla and maxilla.

- 8. The multiple carpal ossifications. Two or three carpals are common in the European pachypleurosaurs and Chinese pachypleurosaur-like forms. There are six carpals in *Dawazisaurus*, including the ossification of the fifth distal carpal. Among non-pistosauroid sauropterygians, available evidence shows that only a few specimens of *Lariosaurus* have six carpal ossifications including the distal carpal 5 (Rieppel, 1998b).
- 9. The retroarticular process. An elongate retroarticular process is common in pachypleurosaurs or like forms. However, the presence of a fossa or a ridge on the dorsal surface of the process is not always the case. As in *Qianxisaurus* and *Wumengosaurus*, the process bears a ridge rather than a fossa in *Dawazisaurus* but the process itself tapers off rather than truncated distally in the former two.

PHYLOGENETIC RELATIONSHIPS

As mentioned earlier, phylogenetic relationships on the Chinese pachypleurosaur-like forms have been controversial. Tow latest works (Cheng et al., 2012a; Sato et al., 2013) essentially supported Holmes et al. (2008), Wu et al. (2011), and Shang et al. (2011) in that the European pachypleurosaurs and those adequately preserved Chinese pachypleurosaur-like forms do not form a monophyletic clade but they are separately grouped with the Nothosauroidea at different levels. These results are conflict with those derived from phylogenies by Jiang et al. (2008) or Liu et al. (2011) in which the Chinese forms (Keichousaurus, Dianopachysaurus, and *Wumengosaurus*) were considered to be closely related to the European pachypleurosaurs and

the Nothosauroidea was the sister-group of the Pistosauroidea. However, the results of Cheng et al. (2012a) and Sato et al. (2013) were partly similar to those of Neenan et al. (2013), i.e., the Nothosauroidea is not grouped with the Pistosauroidea but with the monophyletic Pachypleurosauria formed by the European pachypleurosaurs and most of the Chinese pachypleurosaur-like forms the latter included. With the discovery of *Dawazisaurus*, phylogenetic relationships of the Chinese pachypleurosaur-like forms and the monophyly of the Pachypleurosauria can be reanalyzed again.

In the phylogenetic study of *Dawazisaurus*, we used the data matrix of Neenan et al. (2013) which is a modified version from that of Liu at al. (2011) originally derived from that of Rieppel et al. (2002). As mentioned by Cheng et al. (2012a), totally nine pachypleurosaur-like genera were known from China, including six adequately represented genera (*Keichousaurus*, *Hanosaurus, Wumengosaurus, Diandongosaurus, Dianopachysaurus*, and *Qianxisaurus*) and three fragmentary genera (*Kwangsisaurus, Sanchiaosaurus*, and *Chinchenia*). Therefore, with *Dawazisaurus*, there have been 10 Chinese pachypleurosaur-like genera discovered so far. After a revision, our data matrix consisted of 141 characters and 50 taxa, with the addition of a new character and seven more taxa (*Dawazisaurus, Qianxisaurus*, the three fragmentary taxa as well as the two species of a newly described saurosphargid, *Largocephalosaurus* (*L. polycarpon* Cheng et al., 2012b and *L. qianensis* Li et al., 2013). Changes in the description of some characters and character scoring for certain taxa were explained in Appendix 1 (also see Supplementary Information for the data matrix and the descriptions of all 141 characters).

The revised data matrix was analyzed using PAUP* 4.0 beta 10 (Swofford, 2002). We practiced two analyses to compare with the phylogenetic results obtained in previous studies. A

heuristic search with all taxa and all characters unordered and equally weighted produced 34 most parsimonious trees (MPTs) in the first analysis, with a tree length of 621 steps, a CI of 0.3076, and a RI of 0.6574. As shown in the consensus of the 34 MPTs (Fig. 5A), phylogenetic relationships of the included groups are most similar to those of Neenan et al. (2013:fig. 3) among previous studies. Compared with the latter, phylogenetic relationships within the Eosauropterygia are much better resolved even though the three fragmentary taxa were included (Kwangsisaurus, Sanchiaosaurus, and Chinchenia). Besides the recognition of the monophyletic Pistosauroidea (sensu Neenan et al., 2013) and Nothosauroidea, interrelationships were also fully established for seven genera (including two European forms) of the Pachypleurosauria (Fig. 5A); the latter is not the case in Neenan et al. (2013) in which only five pachypleurosaurs (two European and three Chinese forms, respectively) were included. *Dawazisaurus* is a pachypleurosaur and the basal-most member of the Pachypleurosauria. This was supported by 11 synapomorphies including six unequivocal character states (see Fig. 5A for details). As for the three fragmentary taxa, *Chinchenia* and *Kwangsisaurus* are closely related to the Pachypleurosauria after *Diandongosaurus* within a clade (A in Fig. 5A) and *Sanchiaosaurus* to the Nothosauroidea, which differ from the restudy of Rieppel (1999) in which the former two were suggested to be related to *Corosaurus* within the Pistosauroidea and the latter one to a clade including the European pachypleurosaurs and Nothosauroidea. In addition, phylogenetic relationships of Eusauropterygia-Hanosaurus clade and Helveticosaurus were not resolved in this analysis, unlike in Neenan et al. (2013).

As pointed out earlier, *Kwangsisaurus, Sanchiaosaurus,* and *Chinchenia* were not considered in the study of Neenan et al. (2013) and nor in those studies of Jiang et al. (2008)

and Liu et al. (2011) owing to their fragmentary nature. In order to test the effect of the fragmentary taxa in establishing the phylogeny of the Eosauropterygia, we did the second analysis of the data set with the exclusion of Kwangsisaurus, Sanchiaosaurus, and Chinchenia. The reduced data matrix was analyzed using PAUP* 4.0 beta 10 (Swofford, 2002) with the same setting as those in the first. This analysis yielded four MPTs, with a tree length of 608 steps, a CI of 0.3141, and a RI of 0.6632. Compared with the first analysis, the phylogenetic relationships among the non-eosauropterygian groups differ in that Corosaurus and Cymatosaurus were successively related to the Pistosauroidea of Neenan et al. (2013) and that *Eusauropterygia-Hanosaurus* clade and *Helveticosaurus* formed a monophyletic clade after the Saurosphargidae (Fig. 5B). For interrelationships within the Eosauropterygia, they were very different from those of the first analysis. The most striking is that the seven pachypleurosaurs failed to form a monophyletic group; of them one (*Wumengosaurus*), with *Diandongosaurus*, formed successive sister-groups of the Pistosauroidea within a clade (A in Fig. 5B) and the other six were grouped together with the Nothosauroidea at different levels in another clade (B in Fig. 5B). Regarding interrelationships within the Eosauroptervgia, the results of the second analysis are more comparable to those of Cheng et al. (2012a) and Sato et al. (2013) than others in that the monophyletic Pachypleurosauria could not be established and most members of the group were closely related to the Nothosauroidea.

DISCUSSION

The inclusion or exclusion of the fragmentary Chinese forms did affect the phylogenetic pattern of the Eosauropterygia, unlike in Cheng et al. (2012a). It is interesting that the inclusion of the fragmentary taxa produced a better resolution for the phylogeny of the group than that the exclusion of those taxa did. This suggests that the monophyly of the Pachypleurosauria and its relationships with other eosauropterygian groups obtained by this study is still not stable, which can be further demonstrated by a low bootstrap supporting value to the clade (see Fig. 5). In other words, it would be not surprised that interrelationships among eosauropterygians would change when new forms or better materials of those fragmentary taxa are discovered. On the other hand, this study once more confirmed that certain subgroups of the Sauropterygia such as the Placodontia, Nothosauridae (sensu Rieppel, 1998a) and Pistosauroidea (sensu Neenan et al., 2013) and the Saurosphargidae (sensu Li et al., 2013) are phylogenetically stable, with a high bootstrap support value: 76-79%, 92-95%, 95-98%, and 96%-99%, respectively (Fig. 5) and that the Saurosphargidae, Thalattosauria, and Ichthyopterygia are successively close to the Sauropterygia as in the recent studies (Li et al., 2013; Neenan et al., 2013; Cheng et al., 2014). In addition, this study also indicates that all included Mesozoic aquatic lineages of reptiles can be grouped together as a monophyletic clade which had a relatively high bootstrap support value of 65% or 76% in the two analyses, respectively. This also the case in the most recent studies in which the Ichthyopterygia was included (Li et al., 2013; Neenan et al., 2013; Cheng et al., 2014). Although the phylogenetic position of *Dawazisaurus* is not congruent between the two analyses, it may have had a closer relationship with *Keichousaurus* or *Dianopachysaurus* than others, as suggested by the 50% majority rule consensus obtained by the second analysis; i.e., the three taxa formed a monophyletic trichotomy clade supported by four synapomorphies

including three unequivocal states: the maxilla with one or two enlarged teeth, character 67(0); the dorsal ribs pachyostotic, Character 87(1), and the presence of more than three carpals.

As for the origin of the Pachypleurosauria or pachypleurosaur-like forms, the study of Neenan et al. (2013) appears to imply an eastern Tethyan (Asian) origin because the sistergroup (*Diandongosaurus*) of the clade came from China (see Neenan et al., 2013:fig.3). This was also confirmed here: the sister-group and basal most members of the Pachypleurosauria in the first analysis all came from China and the Chinese forms separately formed the basal most members of the two clades of the Eosauropterygia in the second analysis.

ACKNOWLEDGMENTS

We are grateful to Paleowonder Fossil and Mineral Museum (Taipei) for their skillful preparation of the specimens used in this study and for providing generous assistance during this project. We think C. Li and Q.-h. Shang of IVPP for providing information on some Chinese specimens in their care. X.-c.W particularly wishes to thank the Department of Geology of NMNS for their hospitality during his visits. This work was supported by research grants from the NMNS and the National Science Council, Taiwan (NSC-95-2116-M-178-001) (to Y.-n.C); from the CMN (RCP09 to X.-c.W); and Tokyo Gakugei University (to T.S).

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FIGURE CAPTIONS

FIGURE 1. Skeleton of *Dawazisaurus brevis* gen. et sp. nov. (NMNS000933-F034397). **A**, The whole skeleton in dorsal view; **B**, last three caudal vertebrae in left lateral view; **C**, **D**, a photo and a line drawing of the skull in dorsal view. See the introduction for abbreviations. [planned for page width]

FIGURE 2. Partial skull and mandible and cervical vertebrae 6 to 8 of *Dawazisaurus brevis* gen. et sp. nov. (NMNS000933-F034397). **A**, A photo of the anterolateral side of the skull and mandible in left lateral view; **B**, a photo of the temporal region of the skull and mandible in left lateral view; **C**, **D**, a photo and a line drawing of cervical vertebrae 6 to 9 in dorsal view. See the introduction for abbreviations. [planned for page width]

FIGURE 3. Partial postcranial skeleton of *Dawazisaurus brevis* gen. et sp. nov.
(NMNS000933-F034397). A, Pectoral girdles with anterior dorsal vertebrae in dorsa view;
B, the mid dorsal vertebrae in dorsal view, showing small zygapophyses; C, D, a photo and a line drawing of the pelvic girdle in dorsal view. See the introduction for abbreviations.
[planned for page width]

FIGURE 4. Anterior tail and limbs of *Dawazisaurus brevis* gen. et sp. nov. (NMNS000933-F034397). **A**, Anterior tail in dorsal view, showing the pachyostotic caudal ribs; **B**, **D**, the forelimbs, showing the ossification of distal carpal 5 in **D**; **C**, **E**, **F**, the hindlimbs, showing proximo-internal structures of the right femur in **E**. See the introduction for abbreviations. [planned for page width]

FIGURE 5. Strict consensus trees based on the two analyses of the study, depicting the phylogenetic relationships of *Dawazisaurus* within the Eosauropterygia. A, Derived from 34 MPTs of the first analysis; **B**, derived from 4 MPTs of the second analysis with the exclusion of Kwangsisaurus, Sanchiaosaurus, and Chinchenia. Numbers indicate the bootstrap support values; clades without numbers have a bootstrap support value lower than 50%; dash line with arrow head pointing the Pistosauroidea (sensu Neenan et al., 2013). See Supplementary Information for taxa representing the Saurosphargidae (three), Turtle (two), Lepidosauromorpha (three), and Archosauromorpha (five). Abbreviations: Anaro, Anarosaurus; **Dactylo**, Dactylosaurus; **Neustic**, Neusticosaurus; **Serpiano**, Serpianosaurus. Taxa with asterisk are the Chinese forms. Synapomorphies, as optimized under accelerated (ACCTRAN) transformation assumptions in tree 1 of the 34 MPTs and 4 MPTs separately obtained by the first and the second analyses, are listed for relevant clades, respectively (unequivocal character states labeled by asterisk): Pachypleurosauria in A, characters $1^{*}(1)$, $3^{*}(0), 7^{*}(0), 10(0), 23^{*}(0), 49(0), 53(1), 59(0), 72(1), 75^{*}(1), and 87^{*}(1); Clade B in B,$ characters 1*(1), 43*(2), 49(0), 59(0), 72*(1), 75*(1), 112(0), and 127(2). [planned for page width]

Table 1. Selected measurements (in mm) of *Dawazisaurus brevis* gen. et sp. nov. (L), left.Metacarpals and metatarsals from the right side; *, estimated.

Measurements	NMNS000933-F034397	
Total length of the specimen	423.8	
Presacral length (with skull)	236	
Sacral length	19.8	
Tail length	168.0	
Midline length of skull	36	
Preorbital length	16	
Postorbital length	11	
Length anterior to external naris	8	
Length posterior to external naris	5*	
Mandibular length	50	
Orbital length	10	
Orbital width	7.6	
Supratemporal length	10	
Supratemporal width	4.5	

Humerus length	26.5	
Ulna length	15	
Radius length	14.8	
Length of metacarpal I	2.5*	
Π	5	
III	6	
IV	5.5	
V	4	
Femur length	36.5	
Tibia length	16.2	
Fibula length	16	
Length of metatarsal I	3.8	
II	7	
III	8.5	
IV	8.5	

V	7.5	

APPENDIX 1. To analyze the phylogenetic relationships of *Dawazisaurus*, we used the data matrix of Neenan et al. (2013) with a slight modification. The modified data matrix consists of 141 characters and 50 taxa, with the addition of a new character from Li et al. (2011, 2013) and seven more taxa: *Dawazisaurus*, *Qianxisaurus*, three fragmentary taxa (*Kwangsisaurus*, *Sanchiaosaurus*, and *Chinchenia*) as well as the two species of a newly reported saurosphargid, *Largocephalosaurus* (*L. polycarpon* Cheng et al., 2012b and *L. qianensis* Li et al., 2013). The following includes the new character and changes in the description of a character, coding changes for some taxa, and character scoring for the newly added taxa.

New Character

141. Marginal teeth with convex (0) or concave (1) lingual surface of crown.(Character 149 of Li et al., 2011, 2013)

Characters modified

87. Pachyostosis of dorsal ribs: absent (0); present (1); dorsal ribs stout and broadened to contact each other to form a close 'basket' in lateral view (2). State 2 for saurosphargids.

Coding changes based on our personal observations of the true specimens. ZMNH, Zhejiang Museum of Natural History.

Sinosaurosphargis (IVPP V 17040, ZMNH M 8797, an uncatalogued specimen of ZMNH): characters 2 from (0) to (1); 24 from (0) to (3); 27 from (1) to (0); 75 from (1) to

(0); 84 from (1) to (0); 87 from (1) to (2); 88 to 90 from (?) to (0, 1, 0), respectively; 97 and 98 from (0) to (1); 101 from (?) to (2). *Diandongosaurus* (IVPP V 17761, NMNS00093-F034398; Sato et al., 2013): characters 40, 44, 45, 48, 49, 59, 69, 98, and 102 from (?) to (1); 50-54, 56, and 103 from (?) to (0); 68 from (2) to (0); 140 from (?) to (3).

Character scores for newly added taxa. Data of *Qianxisaurus*, *Chinchenia*, *Kwangsisaurus*, and *Sanchiaosaurus* are derived from Cheng et al. (2012a), and data of the two species of *Largocephalosaurus* from Li et al. (2013).

Dawazisaurus

Qianxisaurus

111010100020000101000000111030210001110?00201??1???????00?100?00010?1010? 10?01000?101021000011?11???1010111001?11301023011?0??112110110001?0

Characters 29 from (4) to (3) and 59 from (0) to (?) in comparison with Cheng et

al. (2012 – characters 31 and 51)

Largocephalosaurus qianensis

Characters 75 from (?) to (0), and 87 from (1) to (2), and 97 from (0) to (1) in

comparison with Li et al. (2013 - characters 69, 72, and 80).

Largocephalosaurus polycarpon

0??1011?1002110?0111?01???11?0???001??12111010???00111011011011?1

Characters 22 from (2) to (?), 75 from (?) to (0), and 87 from (1) to (2) in

comparison with Li et al. (2013 – characters 17, 69, and 72).

Chinchenia

Kwangsisaurus

Sanchiaosaurus



FIGURE 1. Skeleton of Dawazisaurus brevis gen. et sp. nov. (NMNS000933-F034397). A, The whole skeleton in dorsal view; B, last three caudal vertebrae in left lateral view; C, D, a photo and a line drawing of the skull in dorsal view. See the introduction for abbreviations. [planned for page width] 182x228mm (300 x 300 DPI)



FIGURE 2. Partial skull and mandible and cervical vertebrae 6 to 8 of Dawazisaurus brevis gen. et sp. nov. (NMNS000933-F034397). A, A photo of the anterolateral side of the skull and mandible in left lateral view; B, a photo of the temporal region of the skull and mandible in left lateral view; C, D, a photo and a line drawing of cervical vertebrae 6 to 9 in dorsal view. See the introduction for abbreviations. [planned for page width]

182x186mm (300 x 300 DPI)





FIGURE 3. Partial postcranial skeleton of Dawazisaurus brevis gen. et sp. nov. (NMNS000933-F034397). A, Pectoral girdles with anterior dorsal vertebrae in dorsa view; B, the mid dorsal vertebrae in dorsal view, showing small zygapophyses; C, D, a photo and a line drawing of the pelvic girdle in dorsal view. See the introduction for abbreviations. [planned for page width] 182x160mm (300 x 300 DPI)



FIGURE 4. Anterior tail and limbs of Dawazisaurus brevis gen. et sp. nov. (NMNS000933-F034397). A, Anterior tail in dorsal view, showing the pachyostotic caudal ribs; B, D, the forelimbs, showing the ossification of distal carpal 5 in D; C, E, F, the hindlimbs, showing proximo-internal structures of the right femur in E. See the introduction for abbreviations. [planned for page width] 182x196mm (300 x 300 DPI)





FIGURE 5. Strict consensus trees based on the two analyses of the study, depicting the phylogenetic relationships of Dawazisaurus within the Eosauropterygia. A, Derived from 34 MPTs of the first analysis; B, derived from 4 MPTs of the second analysis with the exclusion of Kwangsisaurus, Sanchiaosaurus, and Chinchenia. Numbers indicate the bootstrap support values; clades without numbers have a bootstrap support value lower than 50%; dash line with arrow head pointing the Pistosauroidea (sensu Neenan et al., 2013). See Supplementary Information for taxa representing the Saurosphargidae (three), Turtle (two), Lepidosauromorpha (three), and Archosauromorpha (five). Abbreviations: Anaro, Anarosaurus; Dactylo, Dactylosaurus; Neustic, Neusticosaurus; Serpiano, Serpianosaurus. Taxa with asterisk are the Chinese forms. Synapomorphies, as optimized under accelerated (ACCTRAN) transformation assumptions in tree 1 of the 34 MPTs and 4 MPTs separately obtained by the first and the second analyses, are listed for relevant clades, respectively (unequivocal character states labeled by asterisk): Pachypleurosauria in A, characters 1*(1), 3*(0), 7*(0), 10(0), 23*(0), 49(0), 53(1), 59(0), 72(1), 75*(1), and 87*(1); Clade B in B, characters 1*(1), 43*(2), 49(0), 59(0), 72*(1), 75*(1), 112(0), and 127(2).. [planned for page width]

182x228mm (300 x 300 DPI)