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DECAPOD CRUSTACEA FROM THE AGRIO FORMATION (LOWER CRETACEOUS) OF THE NEUQUÉN BASIN, ARGENTINA

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Abstract: Two species of decapod crustacean are recorded from the Agua de la Mula Member of the Agrio Formation (Upper Hauterivian – Lower Barremian) of the Neuquén Basin of west-central Argentina, namely *Astacodes falcifer* Bell and a new species of *Palaeohomarus*, *P. pacificus*. The preservation of the specimens is exceptional, some showing delicate compound eyes and a stridulatory apparatus, features rarely found in fossil forms. Many specimens are preserved articulated inside calcareous nodules, within dark-grey shales. The lobster-bearing sediments accumulated in a low-energy marine environment and diagenetic mineralization occurred very rapidly, prior to significant decay, thus allowing exceptional preservation of specimens. *Palaeohomarus* was a rare genus in the Cretaceous with a palaeogeographic distribution restricted to the Mediterranean Tethys, the eastern USA and Madagascar, while *Astacodes falcifer* has been recorded only from Speeton (eastern England) and Neuquén.

Key words: Crustacea, Lower Cretaceous, Argentina, exceptional preservation, eyes, stridulatory structure.

THE Neuquén Basin of west-central Argentina is famous for its excellent outcrops of marine Lower Cretaceous rocks and the quality of the fossil record. Although molluscs predominate, remains of decapod crustaceans are locally common. A study of the Cretaceous Crustacea of Argentina published two decades ago (Aguirre-Urreta 1989) included the systematic description of fossil taxa known at that time. More recently, a short review was also published (Aguirre-Urreta 2003). The aim of this study is to record two decapod species, one of them new, on the basis of new specimens from the Agrio Formation of the Neuquén Basin. The quality of preservation allows the description of features not usually preserved in fossils, such as compound eyes and stridulatory structures. The recognition of a taxon that is known from the Northern Hemisphere has interesting palaeobiogeographic implications.

STRATIGRAPHY AND LOCALITIES

The Neuquén Basin (34°–39°30′S), located in the eastern foothills of the Andes, is an important Meso-Cenozoic depocentre, which developed on a convergent continental margin (Legarreta and Uliana 1991) and formed a large north-west–south-east orientated marine embayment (Fig. 1A). This embayment was land-locked towards the east and south but was connected to the Pacific Ocean to the west through an active volcanic arc during most of its Mesozoic history. From the Late Jurassic to the Early Cretaceous, more than 2500 m of mostly marine sedimentary rocks accumulated (Fig. 1B), interfingering with volcanic and volcaniclastic rocks to the west.

Particularly during the late Early Valanginian, a relative rise in sea level extended the coastline quickly towards the continent, and during this transgression, deposition of the Agrio Formation commenced (Weaver 1931; Legarreta and Gulisano 1989). In more basinal areas, the formation is up to 1300 m thick, and here it is divided into three members: Pilmatué, Avilé and Agua de la Mula (Weaver 1931; Leanza *et al.* 2001). The Pilmatué and Agua de la Mula members consist of shales, siltstones, sandstones and limestones of marine origin. They represent mixed clastic–carbonate sedimentation in shoreface to offshore palaeoenvironments on a storm-dominated, shallow-marine ramp (Spalletti *et al.* 2001; Lazo 2004). The intervening Avilé Member (20–100 m in thickness) is a continental sandstone (fluvial to aeolian) that accumulated over the Pilmatué Member

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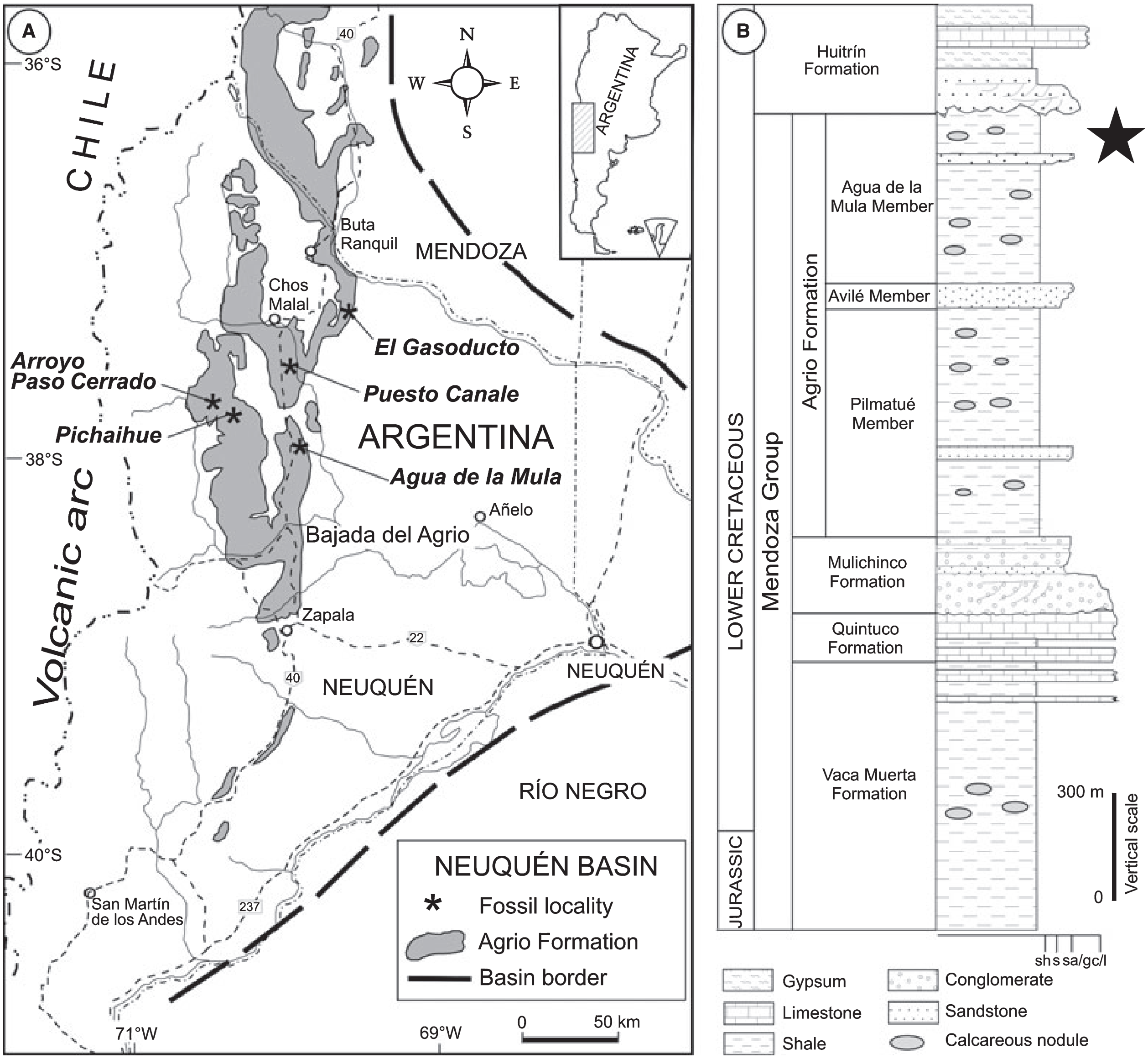

FIG. 1. The Neuquén Basin in west-central Argentina (34°–39°30′ SL), showing localities and outcrops of the Agrio Formation (A); and stratigraphic column of the Upper Jurassic–Lower Cretaceous succession (B); an asterisk marks the interval studied (see Fig. 2).

during a major regression in mid-Hauterivian times (Gulisano and Gutiérrez Pleimling 1988).

The Agrio Formation has an abundant fossil record composed mainly of invertebrates. Ammonites, bivalves, gastropods, nautiloids, corals and serpulids form the bulk of the fossil associations. Bryozoans and echinoids are locally abundant (Lazo 2004; Rodríguez 2007; Taylor *et al.* 2009). Decapod crustaceans are not very common, but do occur throughout the formation, being represented by carcasses, isolated claws and burrowing systems (Aguirre-Urreta 1989, 2003).

All specimens studied here were found in a sequence of dark shales in the uppermost part of the Agua de la Mula Member. At four of the five localities that have yielded lobsters, they are associated with ammonites indicative of a Late Hauterivian – Early Barremian age (Aguirre-Urreta and Rawson 2012). The localities are as follows (Fig. 1A):

1. El Gasoducto, on the western flank of the Curaco anticline, 1.3 km northwest of the intersection of a pipeline and Provincial road 9, and 25 km north of Balsa Huitrín.
2. Puesto Canale, on the right bank of the Río Neuquén, some 9 km east of the junction of an unpaved secondary road with National road 40, in the Naunauco settlement, 32 km south of Chos Malal.
3. Agua de La Mula, a classic section and the stratotype of the Agua de la Mula Member of the Agrio Formation. It lies on the western flank of the Cordillera del

Salado, 80 km south of Chos Malal, with access from National road 40 along a secondary road to a dry oil well.

4. Pichaihue, at the northern end of Sierra Chorriaca. The section lies 2 km southeast of Puesto Rivera, downstream along the Arroyo Pichaihue. Access to Puesto Rivera is by an unmade track from a gravelled secondary road, 12 km east of Colipilli.
5. Arroyo Paso Cerrado, west of Pichaihue, along a track running south off Provincial road 4, some 9 km east of Colipilli.

At Agua de la Mula and Pichaihue, a bed-by-bed analysis of the Agua de la Mula Member was made to document the stratigraphic distribution and facies relationships of the decapod crustaceans; the relevant parts of the succession are illustrated in Figure 2.

SYSTEMATIC PALAEONTOLOGY

Repositories. CPBA, Palaeontology Area, University of Buenos Aires, Pabellón II, Ciudad Universitaria, 1428 Buenos Aires, Argentina; NHM, The Natural History Museum, Department of Palaeontology, London, United Kingdom; SCARB, The Scarborough Museum Trust, Scarborough, United Kingdom.

Order DECAPODA Latreille, 1802
Infraorder ASTACIDEA Latreille, 1802
Family NEPHROPIDAE Dana, 1852

Genus PALAEOHOMARUS Mertin, 1941

Type species. Palaeohomarus hemprichi Mertin, 1941, by original designation (Mertin 1941, p. 188) from the mid-Coniacian (Upper Cretaceous) of northern Germany.

Included species. Besides the type species, *P. brittonestris* (Stenzel, 1945), *P. collignoni* Van Straelen, 1936 and *P. davisi* (Stenzel, 1945).

Diagnosis. Carapace similar to *Hoploparia*, but postcervical groove c runs through a quarter circle forwards, hepatic groove b_1 greatly reduced; abdomen as in *Hoploparia*, first pereiopod heterochelous, with a series of spines on the edge on the outer surface (modified from Mertin 1941, p. 188).

Remarks. De Grave *et al.* (2009) included 19 genera in the family Nephropidae, six of which are known exclusively as fossils and four with extant and fossil representatives, but *Palaeohomarus* was not in their list. This reflects the ongoing discussion among palaeocarcinologists about the validity of the three genera *Hoploparia* M'Coy, 1849, *Palaeohomarus* and *Homarus* Weber, 1795.

Hoploparia is an extinct genus (Valanginian–Miocene) with a nearly worldwide distribution mostly during the Cretaceous, but for many years, there was a significant disagreement among different authors about its validity as a genus distinct from *Homarus*. Pelseneer (1886) indicated that the only difference between *Hoploparia* and *Homarus* was in the rostrum, which was not serrated in the former. Woods (1930) and Van Straelen (1936) both treated *Hoploparia* as a synonym of *Homarus*, while Beurlen and Glaessner (1930) considered that *Homarus* was derived in the Cenozoic from a Cretaceous species of *Hoploparia*. Mertin (1941) extended the range of the latter genus into the Early Cenozoic, when it then gave place to *Homarus*, while *Palaeohomarus* was derived from *Hoploparia* at the end of the Early Cretaceous, dying out during the Late Cretaceous without further descendant. This author considered that the reduction of the cephalic grooves in *Homarus* resembled that in *Palaeohomarus* but that both genera differed so much in the abdomen and first chelipeds that there was not any direct link between them. Glaessner (1960) illustrated a phylogeny where *Hoploparia* led to *Palaeohomarus* and this genus in turn to *Homarus*, and later he (Glaessner 1969) treated *Palaeohomarus* as a subgenus of *Homarus*.

Aguirre-Urreta *et al.* (1991) also discussed the relationships between *Hoploparia*, *Homarus* and *Palaeohomarus*. They concluded that the main differences between the first two genera are the more ornamented carapace in *Hoploparia*, especially the presence of spines and ridges behind the suborbital spine and the greater development of cephalic grooves. This last feature also serves to distinguish *Hoploparia* from *Palaeohomarus*. Williams (1995) analyzed cladistically the relationships among *Hoploparia*, *Palaeohomarus* and *Homarus*, using *Eryma* von Meyer, 1840 as the outgroup. His studies produced a single tree with a consistency index of 100 per cent, in which *Hoploparia* is the sister group of *Palaeohomarus* and *Homarus* (Williams 1995, fig. 5). Tshudy and Babcock (1997) stated that *Palaeohomarus* was a poorly known extinct genus and synonymized it with *Hoploparia*. Although not clearly stated, it seems that this decision prevailed in latter contributions where only *Hoploparia* and *Homarus* are recognized as valid genera (Tshudy and Sorhannus 2000, 2003; Tshudy *et al.* 2005; Feldmann *et al.* 2007; Schweitzer *et al.* 2010, among others).

On the basis of the specimens collected in the Neuquén Basin that present a distinctive pattern and development of cephalic grooves, we here maintain *Palaeohomarus* as a valid genus. It differs from *Hoploparia* in the great reduction in cephalic grooves and from *Homarus* in the more spiny cephalic portion of the carapace and size and shape of the first chelipeds. Most of the morphological features described below follow the terminology of Glaessner (1960) (Fig. 3).

The Neuquén Basin specimens extend the record of *Palaeohomarus* down to the latest Hauterivian or earliest

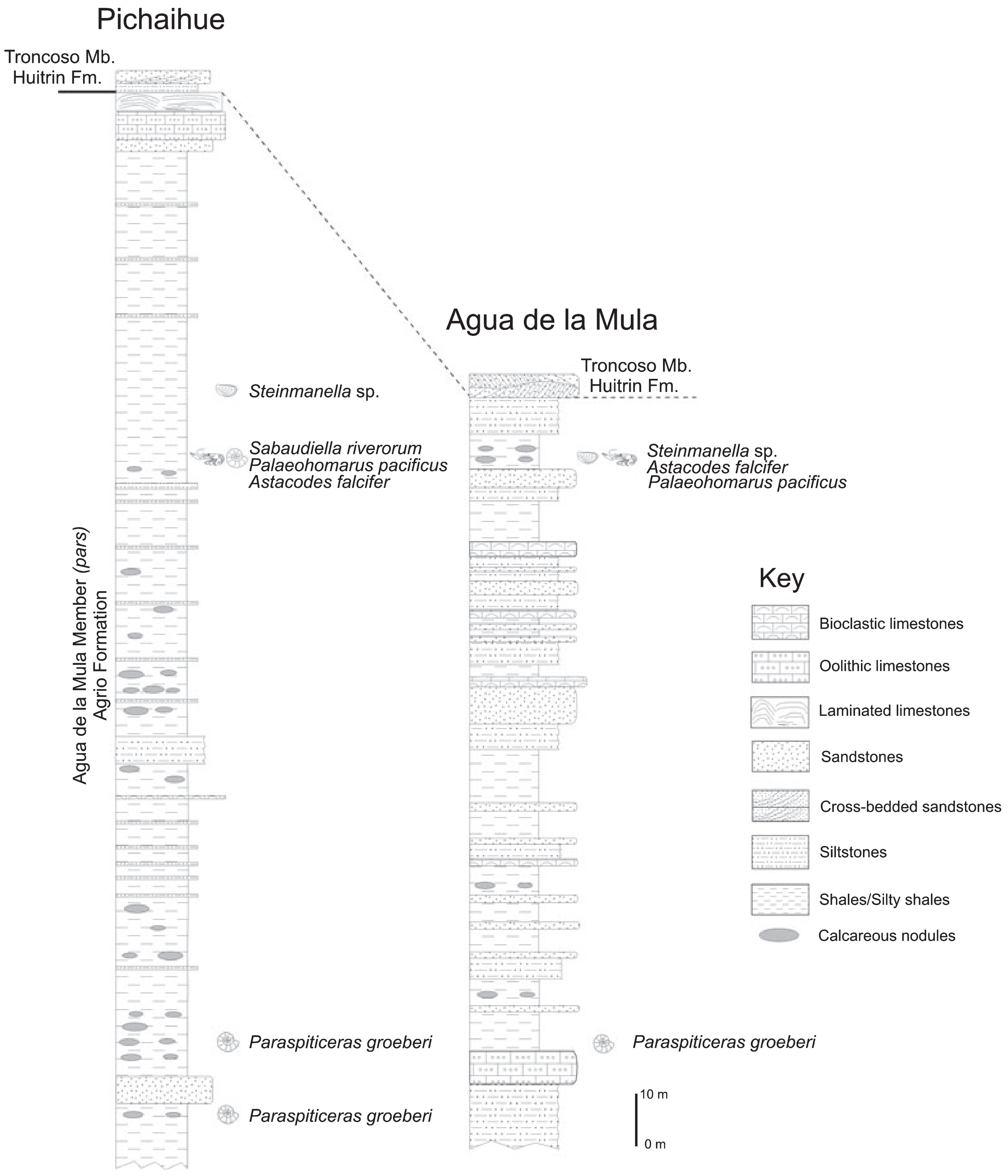

FIG. 2. Lithological column of the upper part of the Agua de la Mula Member (Agrio Formation) at Agua de la Mula and Pichaihue, showing the stratigraphic distribution of decapod crustaceans described here.

Barremian; the oldest previous occurrence is from the Aptian of France (Secretan 1988). *Palaeohomarus* is also known from Albian rocks in Madagascar (Van Straelen 1949; Secretan 1964) and Upper Cretaceous deposits of central and western Europe (Mertin 1941) and Texas (USA) (Stenzel 1945).

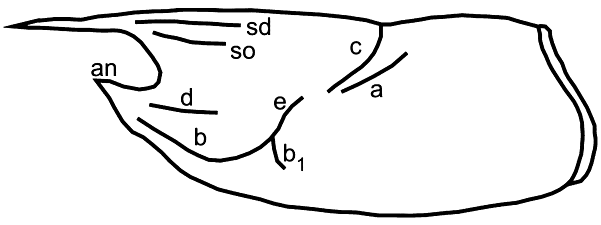

FIG. 3. Line drawing of the cephalothorax of *Palaeohomarus* (modified from Mertin 1941, fig. 12). Terminology of carapace grooves follows Glaessner (1960). Abbreviations: a, branchiocardiac groove; an, antennal spine; b, antennar groove; b_1, hepatic groove; c, postcervical groove; d, gastro-orbital groove; e, cervical groove; sd, subdorsal carina; so, supra-orbital carina.

Palaeohomarus pacificus sp. nov.

Figures 3, 4A–J

Derivation of name. From the Pacific Ocean that flooded the Neuquén Basin in Mesozoic times.

Holotype. Specimen CPBA 20800 from Pichaihue (Fig. 4A–C, E).

Paratypes. A fragmentary specimen from Pichaihue, consisting of part of a cephalothorax (CPBA 20574); two articulated specimens (CPBA 20576–77) from El Gasoducto; one articulated specimen (CPBA 20575) from Agua de La Mula; and one fragmentary specimen consisting of part of a cephalothorax (CPBA 20573) from Puesto Canale.

Type locality and horizon. Pichaihue, Neuquén Basin; Agua de la Mula Member, Agrio Formation, Upper Hauterivian – Lower Barremian.

Diagnosis. Carapace small for genus. Postcervical groove extending downwards and forwards and merging with dorsal end of cervical groove.

Description. Size small for genus. Cephalothorax subcylindrical, broadening towards the posterior end. Anterior region large, 55 per cent of total cephalothorax length measured along mid-dorsal line (from base of rostrum to posterior end). Maximum height nearly on middle of cephalothorax; greatest width on mid-posterior part of branchiostegite. Rostrum bending downwards in front, with a median sulcus. Subdorsal carina (sd) well-defined anteriorly, effacing in the middle of the anterior region, supra-orbital carina (so) terminating anteriorly in a spine, antennal carina very weak beginning on anterior margin with a spine on anterior termination (an). Orbits well defined, bounded by narrow ridge. Left eye oval in shape, partially preserved in holotype (length 3 mm). Postcervical groove (c) very well defined, deep, transverse in dorsal view, extending downwards and forwards, and merging with dorsal end of cervical groove (e), which is well developed only ventrally, deep and narrow. Cervical groove merges into antennar groove (b) that nearly reaches frontal part of carapace. Hepatic groove (b_1) very short and narrow. Gastro-orbital groove (d) represented by a shallow depression. Branchiocardiac groove (a) short, coalescing with postcervical groove.

Marginal furrow narrow, deep, delimiting prominent rim in posterior margin of carapace, but not well developed on ventral margin. Carapace ornamented with granules, larger on dorsal part of anterior region, smaller and evenly spaced in branchiostegite. A pair of tuberculate ridges extends on dorsal surface up nearly to middle of anterior region. Abdomen covered by small pits. First segment small, with reduced pleuron; second segment largest, third to fifth decreasing progressively in size, sixth somite subtrapezoidal. Pleuron of second somite largest, cordiform; pleura of third to fifth somites subtriangular, with a small spine pointing downwards. Uropods oval in shape, exopod with diaresis, telson subquadrate with longitudinal ridges and furrows, posterior border gently rounded, surface pitted. Small, blade-shaped scaphocerite of right antenna preserved. First pereiopod incomplete. Palmar part of propodus longer than wide, inner margin with a carina bounded by a furrow that continues on fixed finger, longer than manus, with straight cutting edge. Dactylus not preserved. Other walking legs fragmentary and poorly preserved.

Remarks. There are no other contemporary species to compare with *Palaeohomarus pacificus* sp. nov. *Palaeohomarus* cf. *hemprichi* from the Aptian of France (Secretan 1988) differs in its much larger size, better development of the cervical groove, a more anterior position of the postcervical groove and a less-marked branchiocardiac groove. Those specimens of *P. collignoni* from the Albian of Madagascar that are of similar size to *P. pacificus* sp. nov. have a similar ornament but can be separated by the configuration of the postcervical and cervical grooves and the shape of the second abdominal pleuron (Van Straelen 1949; Secretan 1964). *Palaeohomarus brittonestris* from the Turonian of Texas compares well in dimensions and ornament with *P. pacificus* sp. nov. but differs in the more impressed postcervical and cervical grooves, which do not merge, and in the hook-shaped hepatic groove (Stenzel 1945). *Palaeohomarus davisi*, from the same strata and locality as the foregoing species, is much larger, and the anterior part of the carapace has more numerous spines (Stenzel 1945), features that also distinguish it from *P. pacificus* sp. nov.

Isolated claws in calcareous nodules, described by Aguirre-Urreta (1989, p. 528, pl. 57, figs 8–10) as *Hoploparia* sp. B, and erroneously assigned a Berriasian–Early Valanginian age, are preserved in several beds within the Agrio Formation (Lower Valanginian – Lower Barremian) and may well represent *Palaeohomarus*.

Palaeohomarus pacificus sp. nov. is restricted to the uppermost part of the Agua de la Mula Member (Agrio Formation) in the Neuquén Basin, occurring in the *Sabaudiella riverorum* Zone, which is regarded as Late Hauterivian – Early Barremian in age (Aguirre-Urreta and Rawson 2012).

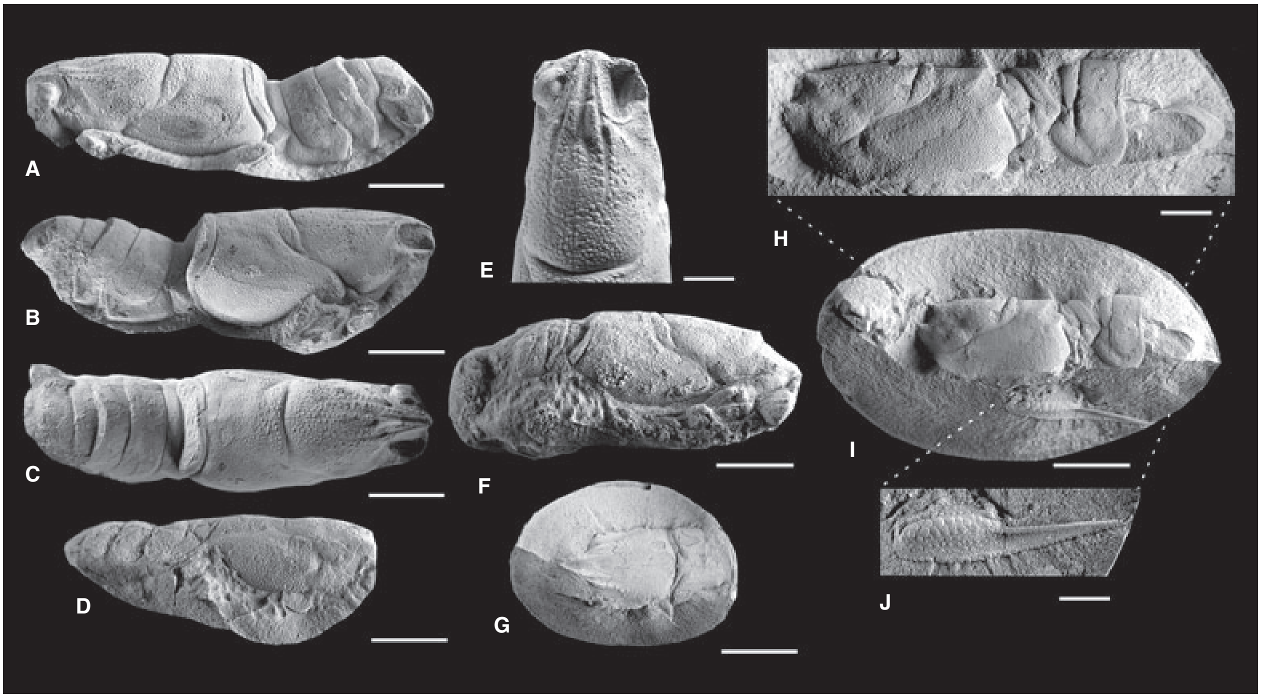

FIG. 4. A–J, *Palaeohomarus pacificus* sp. nov. A–C, lateral and dorsal views of the holotype (CPBA 20800) from Pichaihue. D, lateral view of CPBA 20575 from Agua de la Mula. E, dorsal view of enlarged frontal part of carapace of the holotype, showing left eye and scaphocerite of right antenna. F, lateral view of CPBA 20577 from El Gasoducto. G. dorsal view of CPBA 20573 from Puesto Canale. H–J, lateral views of CPBA 20576 from El Gasoducto. H and J are enlarged views of I. Specimens coated with ammonium chloride prior to photography. Scale bars represent 10 mm.

Infraorder ACHELATA Scholtz and Richter, 1995
Family PALINURIDAE Latreille, 1802

Genus ASTACODES Bell, 1863

Type species. Astacodes falcifer Bell, 1863, by original designation (Bell 1863, p. 30) from the Lower Cretaceous (Hauterivian) of eastern England.

Included species. Besides the type species, *A. davisi* Stenzel 1945, *A. kamptneri* Bachmayer 1959, *A. strambergensis* Bachmayer, 1959, *A. maxwelli* Stenzel, 1945 and *A. woodwardi* (Fritsch *in* Fritsch and Kafka, 1887).

Diagnosis. Resembling *Palinurus*, but rostrum and supraorbital spines of similar length, abdominal terga without transverse grooves (see Glaessner 1969, p. R473).

Remarks. Astacodes originally embraced several fragmentary specimens from the Lower Cretaceous Speeton Clay. Subsequently, Woods (1925) retained only one of Bell's specimens (Bell 1863, pl. 9, figs 1–2) in this genus, while all others were transferred to other genera.

George and Main (1967, fig. 1) divided the Palinuridae into two groups, the Silentes and Stridentes, based on the absence or presence of a stridulating apparatus, and retained three extinct genera as *incertae sedis*. *Astacodes* was placed within the Stridentes, together with another seven genera, and a close relationship with the extant *Palinustus* A. Milne-Edwards, 1880 was indicated on morphological grounds. The preservation of the stridulatory structure in *Astacodes falcifer* described below is the oldest fossil evidence of such a mechanism in palinurids and confirms the view expressed by George and Main (1967).

De Grave *et al.* (2009), in their classification of fossil and living decapod crustaceans, listed 18 genera of palinurids, six known only from the fossil record and five with both extant and fossil species. Of the extinct genera, *Pehuenchia* Rusconi, 1948 should be removed, as it is not a palinurid but a callianassid thalassinidean (Aguirre-Urreta 1989) and *Archaeocarabus* M'Coy, 1849 is a genus that belongs to the Silentes according to George and Main (1967). *Archaeopalinurus* Pinna, 1974 is a Triassic genus from northern Italy (Pinna 1974) and *Palinurina* von Münster, 1839 from the Jurassic of southern Germany is imperfectly known, in particular its carapace and abdomen. *Palaeopalinurus* Bachmayer, 1954 from the Tithonian of southern Germany is only known from fragmentary carapaces. According to Förster (1973), this genus was derived from *Astacodes*, and its peculiar sculpture probably was an adaptation to a certain way of life, details of which were unknown.

The five genera with fossil and extant species comprise one Silentes taxon, *Jasus* Parker, 1883 and four Stridentes: *Linuparus* White, 1847, *Justitia* Holthuis, 1946, *Panulirus* White, 1847 and *Palinurus* Weber, 1795. *Linuparus*, the only other genus with a stridulatory apparatus preserved in fossil examples, is easily distinguished from *Astacodes* by its carapace with three longitudinal ridges, no rostrum and supra-orbital spines close to the median line (Glaessner 1969; Feldmann and Bearlin 1988). The carapace of *Justitia* is ornamented with a strong, scale-like sculpture, and the abdomen has four or five conspicuous transverse grooves on each somite (Holthuis 1991). *Panulirus* has large supra-orbital spines and a strongly ornamented, spiny carapace (Holthuis 1991). Finally, *Palinurus*, as already noted by Glaessner (1969), is similar to *Astacodes*, but differs in having smaller eyes and larger supra-orbital spines.

According to Förster (1973), *Astacodes* ranged from the Late Jurassic to the Late Cretaceous, being represented by seven species in Europe and North America. In addition, there are three other Cretaceous records, all in open nomenclature, from Australia (J. T. Woods 1957), Mexico (Vega *et al.* 2006) and Germany (Mertin 1941).

Astacodes falcifer Bell, 1863
Figures 5A–O, 6A–B

1863 *Astacodes falcifer* Bell, p. 30, pl. 9, figs 1–2 (*non* figs 3–6).
1925 *Astacodes falcifer* Bell; H. Woods, p. 34, pl. 8, figs 3–4; pl. 9, figs 1–5.
?1977 *Astacodes* sp. cf. *A. maxwelli* Stenzel; Alencaster, p. 75, figs 2–3.
?2006 *Astacodes* sp. Vega, Nyborg and Perrilliat, p. 83, fig. 1.5.

Lectotype. Bell (1863, p. 30, pl. 9, figs 1–6) assigned five fragmentary specimens to *Astacodes falcifer* without designating a type. H. Woods (1925, p. 34) subsequently excluded four of them from *A. falcifer* and referred to the remaining specimen (i.e. Bell 1863, p. 30, pl. 9, figs 1–2) as the 'Type', and this is therefore taken as lectotype designation. This specimen, NHM 42238, is from the Speeton Clay of Speeton, eastern England, probably of Hauterivian age.

Material. A single articulated specimen (CPBA 20579), consisting of the cephalothorax and most of the abdomen, from Agua de la Mula; nine specimens, including articulated and quite complete specimens to fragmentary cephalothoraxes from Pichaihue (CPBA 20580–88), one specimen from El Gasoducto (CPBA 20592) and three from Arroyo Paso Cerrado (CPBA 20589–91).

Description. Cephalothorax elongate, greatest width halfway between posterior groove and posterior end. Carapace rounded to slightly depressed in cross-section. Supra-orbital spines large, widely separated, laterally compressed, extending backwards as ridges. Frontal margin concave, rostrum very small. Eyes large, reniform, with square facets and strong pedunculum. Gastric region convex. Postantennal and postorbital carinae with small spines. Mid-dorsal part of cervical groove transverse, lateral parts bending forwards at an obtuse angle. Branchiocardiac groove shallow, extending backwards halfway between cervical groove and posterior carapace margin. Dorsal surface of carapace ornamented with spiny tubercles, becoming smaller in branchial region. Sternum large, triangular, nearly smooth. Basal element of antennae large, subtriangular, inner margin with plectrum and flap(?), antennal plate large, subtriangular, with well-defined file, conforming stridulatory structure. Abdominal terga convex, ornamented with numerous pits. Pleura subrounded, second largest, with ventral spine pointing backwards. Telson not well preserved, pitted, posterior border gently curved. Uropods oval in shape, poorly preserved. Pereiopods slender, poorly preserved.

Remarks. The specimens described here are nearly identical to the material described by Bell (1863) and H. Woods (1925). Examination of the lectotype, NHM 42238, and two specimens from Speeton housed in the Scarborough Museums Trust's collections, described and illustrated by H. Woods (1925, pl. 8, fig. 3a–b is SCARB:2004:1545; pl. 9, fig. 4a–b, is SCARB:2004:1546), has shown that the main differences are in the strength of carapace ornament. However, this feature seems to be related to the preservation of the specimens. While the Argentinian material is more abraded and preserves only inner layers of the cuticle, the Speeton specimens retain more external cuticle layers, and thus, the tubercles and spines are stronger. Such preservational differences were already noted by H. Woods (1925, p. 35) among his own material. One of these individuals (H. Woods 1925, pl. 9, fig. 3a) shows the left eye preserved. Unfortunately, that specimen, originally housed at the Sedgwick Museum in Cambridge, is currently unavailable for study.

Neither *Astacodes strambergensis* nor *A. kamptneri*, both from the Upper Jurassic of southern Germany, are well preserved. Both differ from *A. falcifer* in their much larger, scale-like tubercles on the entire carapace (Bachmayer 1959; Förster 1973).

Astacodes maxwelli and *A. davisi*, both from the lower Upper Cretaceous of Texas, resemble *A. falcifer* more closely, but can be differentiated by their more spinous keels and spines forming an inverted 'V' in the gastric region (Stenzel 1945). It should be noted here that three specimens of *A. maxwelli* illustrated by Stenzel (1945, pl. 35, fig. 2; pl. 45, figs 4–5) retain large eyes, although these are not described in the text and only mentioned in the plate explanation.

Astacodes woodwardi (see Fritsch *in* Fritsch and Kafka, 1887, p. 22, pl. 2, figs 1–3; pl. 5, fig. 7) from the Upper Cretaceous of southern Germany differs from *A. falcifer*

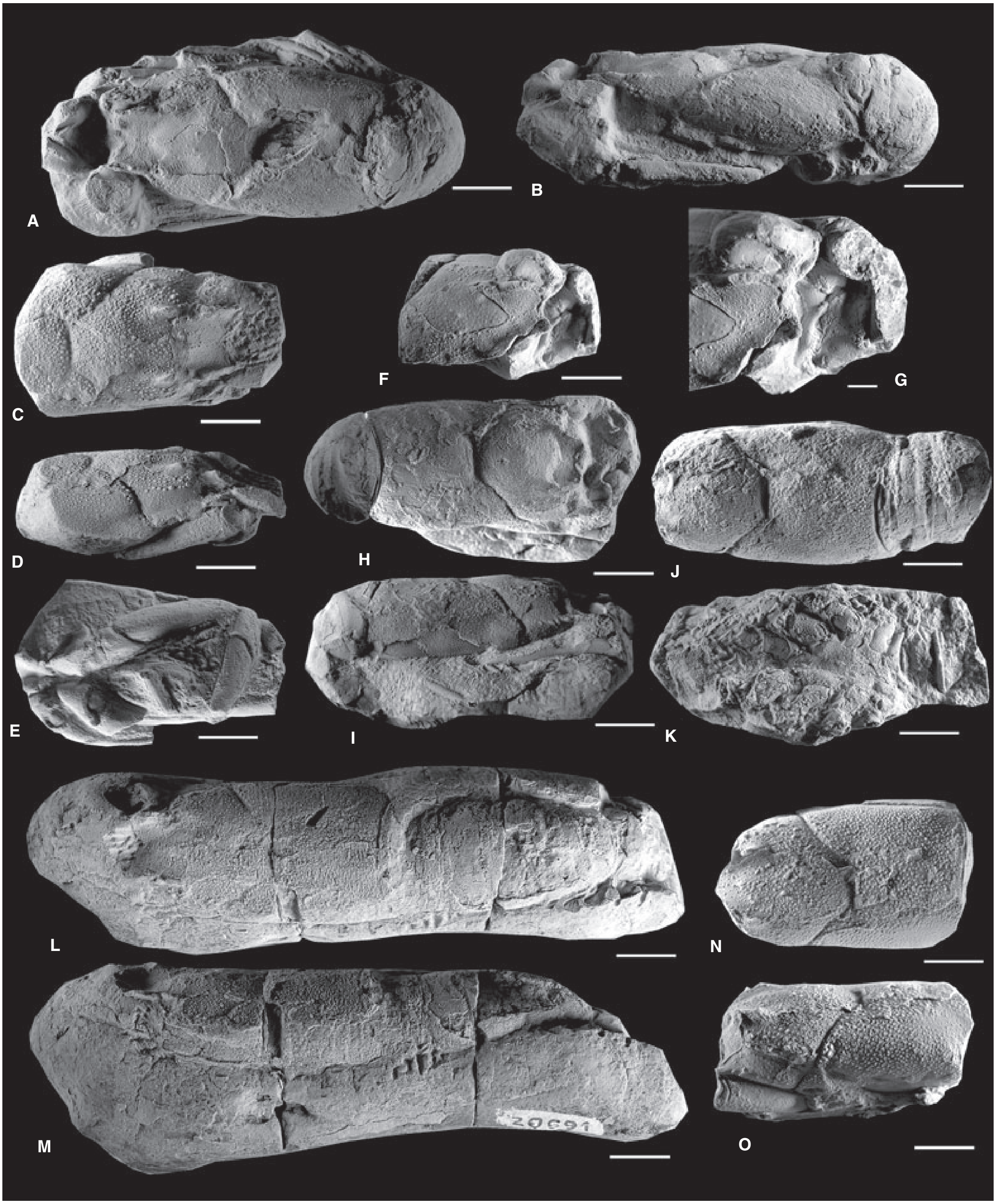

FIG. 5. A–O. *Astacodes falcifer* Bell, 1863. A–B, dorsal and lateral views of CPBA 20579 from Agua de la Mula. C–E, dorsal, lateral and ventral views of CPBA 20583 from Pichaihue. F–G, dorsal views of CPBA 20588 from Pichaihue; G, view of enlarged frontal part of carapace, showing left eye and stridulatory apparatus. H–I, dorsal and lateral views of CPBA 20587 from Pichaihue. J–K, dorsal and ventral views of CPBA 20590 from Arroyo Paso Cerrado. L–M, dorsal and lateral view of CPBA 20591, an unprepared specimen preserved in a burrow from Arroyo Paso Cerrado. N–O, dorsal and lateral views of CPBA 20580 from Pichaihue. Specimens coated with ammonium chloride prior to photography. Scale bars represent 10 mm.

in its very strong and numerous spiny keels in the gastric region.

A single specimen from the Hauterivian–Aptian of Mexico described and illustrated as *Astacodes* sp. cf. *A. maxwelli* by Alencaster (1977) and later refigured by Vega *et al.* (2006), as *Astacodes* sp., is very similar to our specimens in dimensions, ornament and morphology of the ventral region of the cephalothorax.

Astacodes falcifer is known from beds C9A (Lower Hauterivian; P. F. Rawson Collection) and C3 (Upper Hauterivian; H. Woods 1925) at Speeton. Specimens from the Neuquén Basin co-occur with *Palaeohomarus pacificus* sp. nov. in the upper part of the Agua de la Mula Member of Late Hauterivian – Early Barremian age.

MODE OF PRESERVATION AND FACIES RELATIONSHIPS

In comparison with other calcified invertebrates of the Agrio Formation, for example molluscs, decapod crustaceans are rarely recorded, being confined to shales and fine-grained sandstones even though ichnofossils produced by them, such as *Thalassinoides* and *Ophiomorpha* are abundant throughout the unit. The poor body fossil record of decapod crustaceans is largely a consequence of taphonomic bias because of rapid decay (Schäfer 1972). Decapod cuticles are thinner, variably sclerotized and/or calcified and have a greater proportion of organic material than molluscs (see Mutel *et al.* 2008). Thus, cuticles are prone to more rapid decay than molluscan shells under the same environmental and diagenetic conditions. In the studied unit, decapod carcasses have been found exclusively in offshore fine-grained facies. This apparent facies restriction probably is a reflection of taphonomy rather than original habitat preference; rapid decay and destruction occurred mainly in well-oxygenated and agitated sandy substrates typical of nearshore environments. In support of this interpretation, it should be noted that decapod burrowing systems are present in both nearshore and offshore settings.

The mode of preservation of *Astacodes* and *Palaeohomarus* at the top of the Agua de la Mula Member is noteworthy. Most specimens consist of still articulated hard parts, including articulated cephalothorax, abdomen, base of pereiopods and tail fan, while some of them show exceptionally preserved stalked compound eyes with mineralized eye cuticle (Fig. 6). Most carcasses are enclosed in calcareous nodules that have further protected them. In contrast, fragmentary parts of carapaces, usually poorly preserved, may represent remains of moults.

Energy Dispersive Analysis X-Ray (EDAX) performed on some specimens indicates that the stalked eyes are mineralized by calcium phosphate and that the surrounding matrix is mixed, being composed of siliciclastic and carbonate material. The phosphatization of such delicate compound eyes in three dimensions requires very rapid, almost *in vivo*, mineralization, prior to burial, and indicates that diagenesis predated significant decay (see Allison and Briggs 1991).

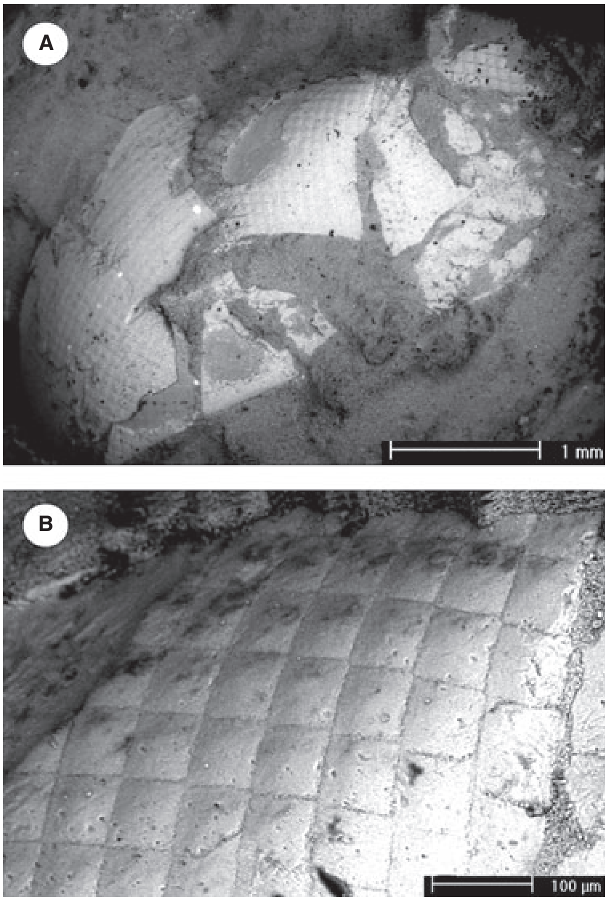

FIG. 6. Scanning electron micrographs of preserved eye of *Astacodes falcifer* Bell, 1863. A, General view of left eye of specimen CPBA 20587 from Pichaihue. B, Enlarged detail of part of the same eye showing the square facets.

The horizon at which the lobsters occur consists of dark-grey shales with distinct bands of calcareous nodules. Smooth, dark-grey coloured nodules predominate, averaging 5–10 cm in horizontal diameter and showing a cylindrical to ovoid shape. Others are slightly irregular in shape, reminiscent of Y- and T-shaped branches belonging to *Thalassinoides* isp. or *Ophiomorpha* isp. burrow systems, and these are thus interpreted as concretionary fragments of those trace fossils. Most nodules are barren, and while some enclose lobsters others include bivalves (small palaeotaxodonts and trigonioids), gastropods, heteromorph ammonites and isolated pycnodontid fish teeth.

The excellent preservation of the lobsters, with articulated cephalothorax, abdomen and proximal segments of walking legs and antennae, and their enclosure within cylindrical nodules reminiscent of decapod burrow systems (Fig. 5L–M) indicates that they probably died within their burrows and remained there during at least the earliest stage of fossilization. The sequence of fossilization would have been as follows: (1) *in vivo* or immediately *post-mortem* secondary phosphatization of eye cuticles in terms of days probably within a burrow system but before the burrows were infilled with sediment; (2) shallow entombment of carcasses within the first centimetres of infilling sediment and closure of the phosphatization window; (3) partial biodegradation and disarticulation of carcasses especially distal segments of antennae, pereiopods and pleopods; and (4) precipitation of mud carbonate around the remaining carcasses to produce a calcareous nodule during a pause in sedimentation at the early diagenetic stage. This occurred before compaction of the sediment because the specimens are almost uncrushed.

Calcareous nodules are usually formed a little below the sediment-water interface during times of low or zero sedimentation rates allowing the carbonate to be produced and inhibiting dilution with siliciclastics (Brett and Baird 1986). An almost zero sedimentation rate also probably enhanced the phosphatization of eye cuticles (Allison 1988).

At Pichaihue, the calcareous nodules with lobsters are near the base of an interval of dark silty shales with occasional thin siltstone streaks, which become more frequent and thicker towards the top. These rocks represent fair-weather suspension deposits of an outer ramp, and the levels with calcareous nodules indicate episodic pauses of sedimentation (Lazo *et al.* 2005). At Agua de la Mula, the calcareous nodules occur at the base of an 8-m-thick bed composed of massive dark-grey shales and silty shales arranged in a coarsening-upwards cycle grading to alternating olive grey mudstones and yellowish fine to medium-grained sandstones showing lenticular and wavy bedding near the top. This interval is interpreted to represent deposition in a proximal offshore setting near storm wave base. Thus, during fair-weather conditions, fall-out deposition occurred, while at other times, there was storm reworking and deposition: these alternating conditions are indicated by the interbedding of the mudstones with thin sandy tempestites (see additional lithofacies data in Lazo *et al.* 2005).

A diverse macrofauna, including the lobsters described here, colonized the soft to firm muddy bottoms during fair-weather conditions. The seafloor was oxygenated, and bottom colonization probably took place as the substrate changed from soupy to soft to firm bottom consistency. Storm events were partially erosional and reworked and mixed benthic organisms. There is no evidence of any hardground or rocky substrates.

PALAEOBIOGEOGRAPHY AND EVOLUTION

Palaeohomarus was a rare genus in the Cretaceous with a palaeogeographic distribution restricted to central and western Europe, the eastern USA and Madagascar. According to Mertin (1941), it was an inhabitant of shallow coastal waters that evolved as an offshoot of *Hoploparia* and died out at the end of the Cretaceous. Glaessener (1960, 1969) accepted the derivation from *Hoploparia* but thought that *Palaeohomarus* gave rise to *Homarus*.

The discovery of *Palaeohomarus* in the Upper Hauterivian – Lower Barremian sediments of the Neuquén Basin, postdating the earliest (Valanginian) records of *Hoploparia*, raises some doubts on the relationships of these three genera of clawed lobsters. It is worth noting here that there are no certain records of *Hoploparia* from the Lower Cretaceous of the Neuquén Basin, except for isolated claws assigned to *Hoploparia* sp. B by Aguirre-Urreta (1989) that probably belonged to *Palaeohomarus*. Instead, *Hoploparia* has been recorded at higher latitudes from other Patagonian basins and from Antarctica (Aguirre-Urreta 1989; Aguirre-Urreta *et al.* 1991; Feldmann *et al.* 1993).

If the criterion that the first occurrence of a taxon represents the area of origin is used, with subsequent pathways of dispersal to regions with later records (Feldmann and Schweitzer 2006), then *Palaeohomarus* should have originated in shallow waters in temperate regions of the southern hemisphere. A gradual reduction in cephalic grooves from an ancestral chilenophoberine such as *Chilenophoberus* Chong and Förster, 1976, known from the Oxfordian of northern Chile, may be a plausible path.

Astacodes is not a very common genus, being represented only in the Late Jurassic–Late Cretaceous of Europe and the Late Cretaceous of the USA, with a dubious record in the Albian of Australia (J. T. Woods 1957). The first known species are all in the Tethys, and the genus probably then dispersed into subtropical and temperate latitudes, both in the northern and southern hemispheres. *Astacodes falcifer* is recorded both from Speeton and Neuquén, but so far from nowhere else. However, *Astacodes* sp. from Mexico (Vega *et al.* 2006) is very close in morphology and age, and could be a good link between those two regions. Such a pattern of distribution is mirrored among Early Cretaceous ammonites as well (Rawson 1999).

Recently, molecular evidence has been used to reconstruct the phylogeny of the Palinuridae with some contrasting results. According to Tsang *et al.* (2009), Stridentes forms a monophyletic assemblage, indicating that the stridulating, sound-producing organ evolved only once in the spiny lobsters while Silentes is paraphyletic. For Palero *et al.* (2009), the monophyly of the Silentes clade was unambiguously determined, and their divergence estimated at 75 Ma, but the monophyly of Stridentes was not strongly supported in their molecular analysis. The recognition of the stridulatory structure in *Astacodes falcifer* from the Upper Hauterivian – Lower Barremian of the Neuquén Basin sheds light on a much earlier development of such a structure and moves back the time of divergence between Stridentes and Silentes to at least 130 Ma. On the basis of molecular studies, Tsang *et al.* (2009) suggested a southern hemisphere origin for the Palinuridae with the subsequent diversification driven by the closure of the Tethys and the formation of the Antarctic circumpolar current. This conclusion did not take into account either the earliest palinurid record from the Triassic of Italy (Pinna 1974) or the numerous Jurassic references from the Tethys.

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